

Snowshoe Hare (*Lepus americanus*): A Technical Conservation Assessment



**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

July 19, 2006

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Peer Review Administered by
[Society for Conservation Biology](#)

Ellsworth, E. and T.D. Reynolds. (2006, July 19). Snowshoe Hare (*Lepus americanus*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: <http://www.fs.fed.us/r2/projects/scp/assessments/snowshoehare.pdf> [date of access].

ACKNOWLEDGMENTS

We are indebted to Dennis Murray for providing a wealth of information and to Patricia A. Isaeff for assembling the Envirogram into a crisp display. Gary Patton made a series of important recommendations that significantly improved this manuscript. Oz Garton helped us with our discussion of sensitivity and elasticity, and we are grateful for the encouragement and assistance offered by Steve Abele, Janet Rachlow, Kerry Reese, and Kathy Strickler.

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COVER PHOTO CREDIT

Snowshoe hare (*Lepus americanus*). South Central Service Cooperative: <http://www.SCSC.k12.ak.us>.

LIST OF ERRATA

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF SNOWSHOE HARE

The population ecology and biology of snowshoe hares (*Lepus americanus*) are well-studied topics in boreal forests of Canada and Alaska, yet relatively little research has been conducted on hares in the Rocky Mountains. For some wildlife species the lack of regionally specific information might not be particularly important, but in this case it is apparent that critical regional differences exist in ecological conditions and population dynamics between boreal and Rocky Mountain hare populations. The Rocky Mountains are much more heterogeneous in terms of climate, topography, and habitat types when compared to boreal forests, and this has a major impact on hare ecology. Hares in the Rocky Mountains use a broad range of forest types, consume a variety of winter browse species, are preyed upon by a large suite of predators, and likely have a different role in community-level dynamics. Their populations also are smaller and patchier, but apparently more stable.

The importance of focused hare research in the Rocky Mountains is further underscored by the recent listing of Canada lynx (*Lynx canadensis*) as threatened in the contiguous United States under the Endangered Species Act (U.S. Fish and Wildlife Service 2000), and by lynx recovery efforts in Colorado. Canada lynx are specialist hare predators in northern regions, and their livelihood in boreal forests is dependent on a minimum threshold density that is estimated to be > 0.5 hares per ha, or that ranges from 1.1 to 1.8 hares per ha. In the western United States, hare population densities that reach these levels tend to be found in comparatively small and medium-size patches of suitable habitat; expansive areas that support abundant hare populations are relatively uncommon. It is not clear whether the size of western hare populations have changed during historic times because there are no long-term data sets of hare populations in southern areas. However, reduced populations of lynx in the West could indicate that their main prey base, snowshoe hares, has declined as well. Furthermore, fire suppression has contributed to a decline in the abundance of young lodgepole pine (*Pinus contorta*) stands, a particularly important habitat for snowshoe hares in at least some western mountains.

In this paper, we emphasize the importance of snowshoe hare conservation in light of Canada lynx requirements and provide management recommendations that could enhance hare habitat quality. In particular, we provide specific management recommendations for two of the most important habitat types for hares in the Rocky Mountains, lodgepole pine and Engelmann spruce - subalpine fir forests (*Picea engelmannii* - *Abies concolor*). Although these species are common associates in subalpine environments, a distinction is made between them because some important differences exist in the dynamics of the ecological relationship with hares. Most importantly, patterns of hare abundance fluctuate in distinctly different ways in spruce-fir and lodgepole pine forests. Overall, hares probably reach a higher density in young lodgepole pine forests, but they are probably more stable over longer time periods in spruce-fir forests.

Hares are abundant in young lodgepole pine forests with a high stem density because cover conditions are good and lodgepole pine is a highly nutritious conifer. However, optimum structural conditions (i.e., dense understory cover) are typically short-lived. As lodgepole forests mature, they self-prune their lower branches and simply do not contain enough understory cover to provide refuge or forage for a high density of hares. In lodgepole pine forests, our primary management recommendation to maintain dense hare populations is to promote the growth of young regenerating stands (via fire in particular).

Conversely, mature spruce and fir tend to retain their crown at low levels, providing food and cover for hares. Consequently, there are fewer apparent benefits to disturbance in spruce-fir forests. In spruce-fir forests, we recommend that managers focus on preserving large blocks of interconnected habitat.

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EDITOR: Gary Patton, USDA Forest Service, Rocky Mountain Region

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INTRODUCTION

This conservation assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS; **Figure 1**). Although the snowshoe hare (*Lepus americanus*) is not listed as a sensitive or endangered species in Region 2, this assessment is warranted because hares are considered a Management Indicator Species (MIS) on at least one national forest in the region, and they are the primary prey item of Canada lynx (*Lynx canadensis*), a species that is federally listed as a threatened species in the contiguous United States (U.S. Fish and Wildlife Service 2000). Persistence of Canada lynx depends upon relatively abundant and well-distributed hare populations, and it is not clear whether the size of hare populations is currently adequate to broadly support sustainable populations of lynx across upper elevation forests of Region 2.

This assessment addresses the biology and ecology of the snowshoe hare throughout its range in Region 2, which is restricted to the mountains of Colorado and Wyoming. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide land managers, research biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop prescriptive management recommendations.

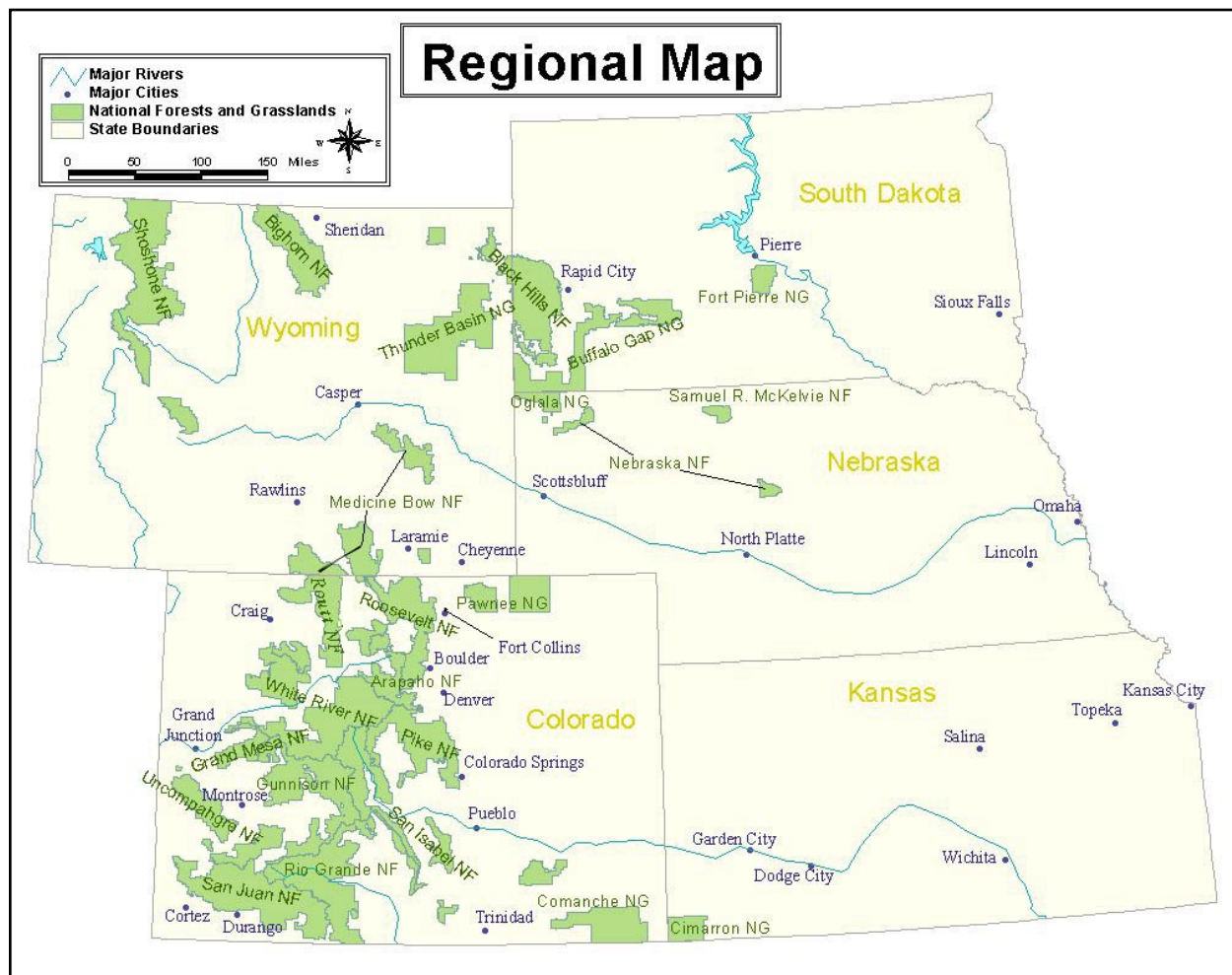


Figure 1. Map showing the boundaries of the USDA Forest Service Rocky Mountain Region, and the lands they administer.

Instead it provides the ecological background upon which management can be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, we cite management recommendations proposed elsewhere and discuss the results of a few studies that implemented specific management practices.

Scope

This conservation assessment examines the biology, ecology, conservation status, and management of the snowshoe hare with specific reference to the geographic and ecological characteristics of the Rocky Mountain Region. Although there is a large amount of literature on this species, most field investigations have been conducted in Canada and very few within Region 2. To place this work in the ecological and social context of the central and southern Rocky Mountains, this document focuses on work that a) is pertinent to general snowshoe hare ecology, b) provides information that is useful for comparative purposes, or c) originated in areas with similar habitat (i.e., studies in other Rocky Mountain states). This document also focuses on characteristics of snowshoe hares in the context of the current environment rather than under historical conditions. The evolutionary environment of this species is considered in conducting the synthesis, but it is placed in a current context.

In producing this assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on snowshoe hares are cited in this assessment, nor are all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. We chose to use some non-refereed literature or reports in the assessment when they provided information unavailable elsewhere. Unpublished data are limited to work from the lead author's unfinished dissertation, which provided information on the winter feeding ecology of hares in a Rocky Mountain setting.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing

with uncertainty. A commonly accepted approach to science is based on progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct experiments that produce clean results in the ecological sciences. Often, we must rely on observations, inference, good thinking, and models to guide our understanding of ecological relations. In this assessment, we note the strength of evidence for particular ideas, and we describe alternative explanations where appropriate.

Publication of Assessment on the World Wide Web

To facilitate their use, species conservation assessments are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More importantly, it facilitates their revision, which will be accomplished based on guidelines established in Region 2.

Peer Review

Conservation assessments developed for the Species Conservation Project have been peer reviewed prior to their release on the Web. This report was reviewed through a process administered by the Society for Conservation Biology, employing two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessments.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Snowshoe hares have a global rank of G5, which means that on a coarse scale the species is common, widespread, and abundant. Within Region 2, hares occur only in Colorado and Wyoming, where they have not been given statewide heritage rankings. However, an isolated hare population in the Bighorn Mountains of northern Wyoming is given a heritage rank of S1, indicating that this population is critically imperiled because of extreme rarity or because some factor makes it highly vulnerable to extinction. In several western states, including Colorado and Wyoming, hares are managed as a game species, and daily bag limits and hunting seasons are established.

Existing Regulatory Mechanisms, Management Plans, Conservation Strategies

No federal regulations exist for snowshoe hares, but they are a Management Indicator Species (MIS) on the White River National Forest in central Colorado. Within the National Forest System, MIS serve as barometers of species viability at the forest level. By monitoring MIS, managers can 1) estimate the effects of planning alternatives on fish and wildlife population [36 CFR 219.19 (a) (1)]; and 2) monitor the effects of management activities on species via changes in population trends [36 CFR 219.19 (a) (6)]. State regulations within Colorado and Wyoming are limited to a hunting season designation and daily bag limits (10 hares per day in Colorado and 4 per day in Wyoming; see Colorado Division of Wildlife and Wyoming Game and Fish). Neither the state of Colorado or Wyoming has a management plan or conservation strategy for snowshoe hares.

The lack of widespread conservation plans for this species is not surprising given that there is no direct evidence that snowshoe hare populations have declined in Colorado or Wyoming. However, it is understood that managing for abundant hare populations is critical for conservation of Canada lynx (Aubry et al. 2000a, Ruediger et al. 2000), a threatened species in the contiguous United States under the Endangered Species Act (U.S. Fish and Wildlife Service 2000). Lynx populations have declined in the contiguous United States in the past century (McKelvey et al. 2000a), and long-term viability of lynx may be intimately linked to snowshoe hares, their primary prey (Ruggiero et al. 2000, Steury and Murray 2004). The USFS is preparing two programmatic amendments to the land and resource management plans of national forests within affected areas of the amendments to incorporate conservation measures for lynx, based largely on the "Lynx Conservation Assessment and Strategy" (Ruediger et al. 2000). A Northern Rockies amendment will include the Shoshone and Bighorn national forests of northern Wyoming; and a Southern Rockies amendment will include all national forests in Colorado and southern Wyoming. An important component of lynx conservation, as outlined in Ruediger et al. (2000), is identification of and management for high-quality snowshoe hare habitat in the western United States. Therefore, one of the goals of our document is to identify important conservation issues concerning hares, and to suggest strategies to preserve and enhance hare populations in the Region 2.

Biology and Ecology

Classification

The snowshoe hare is one of at least 78 recognized species worldwide within the Order Lagomorpha (Angermann et al. 1990, Nowak 1999). Lagomorphs are part of a lineage of placental mammals that includes the rodents, tree shrews, flying lemurs, and primates (Scally et al. 2001). The Order Lagomorpha is further subdivided into two distinct families, Leporidae (hares and rabbits) and Ochotonidae (pikas). Eleven genera and 56 species of leporidae are extant (Angermann et al. 1990), and these occupy most landmasses with the exception of Antarctica and most oceanic islands. The leporidae fall into two major clades, which correspond to the genera *Sylvilagus* (rabbits) and *Lepus* (hares; Ramos 1998). Hares and rabbits are distinguished based on skull and dental morphology (Lyon 1904, Nelson 1909, White and Keller 1984), and on their precocial (hares) or altricial (rabbits) young. Within the genus *Lepus* there is a phylogenetic separation (at least in the most parsimonious of trees they produced) of hares into distinct clades comprised of a) the African hares, b) a western American clade, and c) an arctic clade (Halanych et al. 1999). Snowshoe hares appear to be more closely related to southwestern hares (white-sided jackrabbit [*L. callotis*] and antelope jackrabbit [*L. alleni*]) than the arctic clade of species (*L. arcticus*, *L. othus*, and *L. timidus*; Halanych et al. 1999).

Fifteen subspecies of snowshoe hare are currently recognized in North America based on morphometric analyses and pelage color (Hall 1981). *Lepus americanus bairdii* is the predominant subspecies within Region 2 and other portions of the Rocky Mountains. The only other subspecies in Region 2 is *L. americanus seclusus*, an apparently insular population that occurs in the Bighorn Mountains in north-central Wyoming. However, it is unclear whether *L. americanus seclusus* is indeed taxonomically distinct, and the validity of subspecific classifications of hares to date has questionable merit given that designations were based on pelage color and cranial morphology rather than genetic analyses (Dalquest 1942, Hall 1981). The use of cranial morphology to designate subspecific populations appears to be invalid because hare skulls across North America have continuous rather than non-overlapping morphometric variation (Nagorsen 1985). Resolution of intraspecific taxonomy in snowshoe hares requires additional rigorous genetic efforts.

General species description

Like other hares, snowshoe hares have long ears, powerful hindlegs, bulging eyes, and short tails. Their pelage is white in the winter and brown in the summer although some populations from the Pacific coast of the United States and southern British Columbia retain brown coats in winter (Nagorsen 1983). Snowshoe hares have disproportionately large hind feet (11 to 15 cm), which facilitate movement across the snow surface through reduced foot loading (Keith 1990, Keith and Bloomer 1993). Snowshoe hares are the smallest species of *Lepus* (Keith 1990). Adult body size ranges between 0.9 and 2.3 kg and averages 1.3 kg (Grange 1932, Rowan and Keith 1959, Newson and de Vos 1964). The total length of hares can range from 36 to 52 cm (Banfield 1974, Hall 1981). Females weigh 10 to 25 percent more than males on average (Murray 2003), and adult hares weigh more than juveniles for up to 9 to

11 months following birth (Keith and Windberg 1978). Seasonal fluctuations in body mass are commonly observed, with hares tending to lose weight over the winter. The size of hares also varies regionally. Hares in the Pacific and Rocky Mountain regions are smaller than more northerly and easterly populations (Dalquest 1942, Nagorsen 1985).

Distribution

Snowshoe hares have the most extensive distribution of any North American species of *Lepus*. They occur from the Pacific to Atlantic coast and from northern Canada and Alaska to portions of the Sierra Nevada Mountains, southern Rocky Mountains, Great Lakes region, and the northern Appalachian Mountains (**Figure 2**). Within this broad range, hares occupy a diversity of forest types in several climate zones that range from moderate coastal to the extreme continental

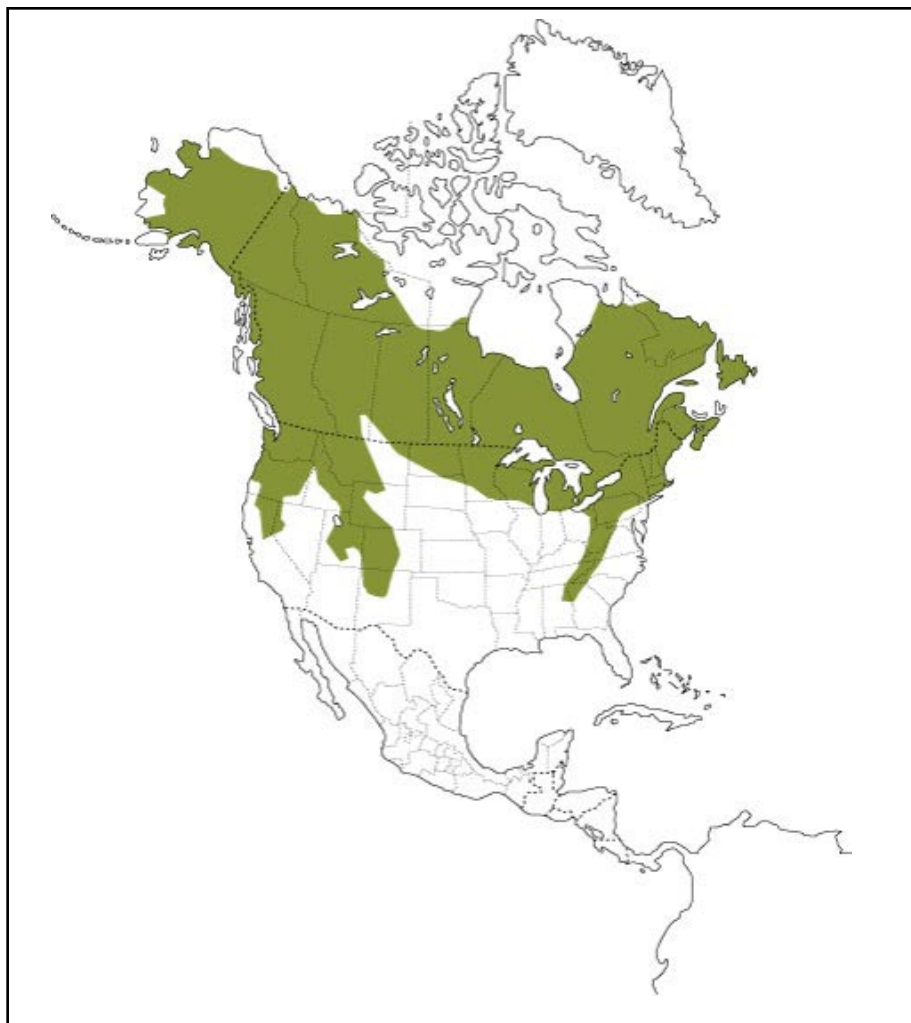


Figure 2. Distribution of the snowshoe hare in North America.

climates of interior Canada. Northern boundaries of this species' range coincide with treeline. It is believed that vulnerability to avian predation in barren areas precludes snowshoe hare colonization (Barta et al. 1989). The southern boundary of the species' range may be determined by climate-driven factors such as reduced depth and duration of snow cover and increasing patchiness of vegetation that result

in increased exposure and vulnerability to predation (Buehler and Keith 1982, Sievert and Keith 1985, Murray and Boutin 1991).

In the Rocky Mountains, the range of the snowshoe hare extends southward through the mountains of Colorado (**Figure 3**), into the northernmost mountains of New Mexico. In the Southern Rocky Mountains,

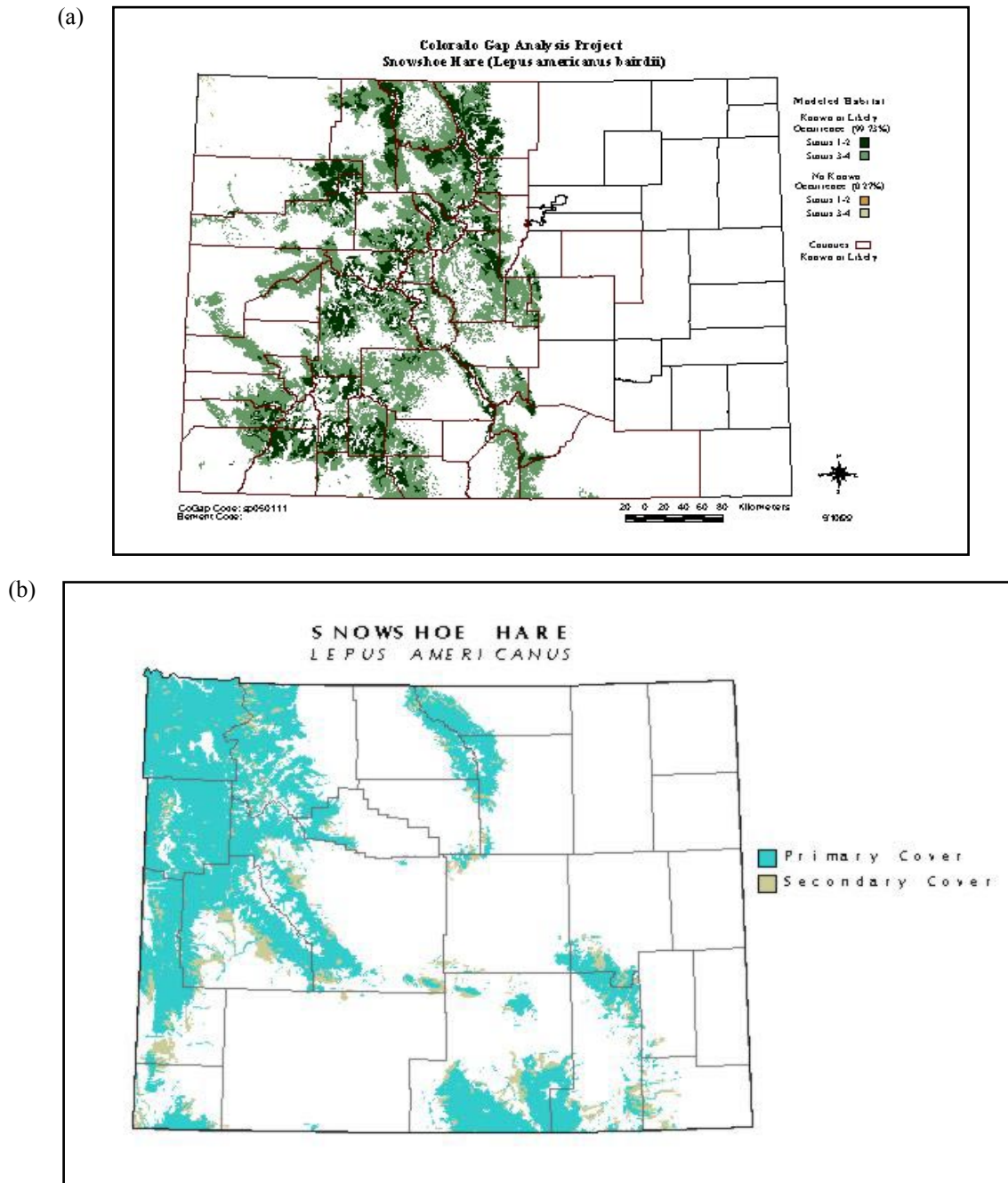


Figure 3. Potential snowshoe hare habitat in (a) Colorado and (b) Wyoming (from Colorado Gap Analysis Project Report <http://ndis1.nrel.colostate.edu/cogap/cogaphome.html> and Wyoming Gap Analysis Project <http://www.sdvc.uwyo.edu/wbn/gap.html>.)

hares are most abundant within higher elevation forests. In Colorado, they are generally present in an elevation band from 2,438 to 3,505 m (Fitzgerald et al. 1994), with the lowest elevation recorded at 1,980 m in Gunnison County (Warren 1942). Hares occur at slightly lower elevations in Wyoming, which is not surprising given that the lower limit of preferred forest types tends to decline with increasing latitude. Hares occupy some relatively isolated mountain ranges such as the Laramie, Granite, and Bighorn Mountains in Wyoming, as well as the Uintah Mountains in Utah and the Sangre de Cristo range in Colorado, but they are absent from seemingly suitable habitat in the Black Hills (South Dakota Natural Heritage Program) and the Pike's Peak massif on the east slope of the Rocky Mountains in Colorado (G. Patton personal communication 2006). County records of occurrence in Colorado prior to 1972 are available in Armstrong (1972).

Population status

Hare abundance and population dynamics in the Rocky Mountains

In the western United States, hare density and relative abundance have been estimated in Colorado (Dolbeer and Clark 1975, Bartmann and Byrne 2001, Zahratka 2004), Idaho (Murray et al. 2002, Wirsing et al. 2002a, E. Ellsworth unpublished data), Montana (Adams 1959, Koehler et al. 1979, Malloy 2000, Griffin 2004, Mills et al. 2005), Oregon (Black 1965, Abele 2004), Utah (Dolbeer and Clark 1975, Anderson et al. 1980, Wolfe et al. 1982), and Washington (Koehler 1990a, b, Quade-leu in prep.). For comparative purposes, the most reliable data are from mark-recapture techniques or fecal pellet counts (see Estimating hare abundance, density, and habitat section) because density estimates can be derived from these methods. Density estimates in the U.S. Rocky Mountains range from 0 to 2.7 hares per ha (**Table 1**), which is within the range of hare densities recorded in northern boreal forests during the cyclic low-phase, but substantially less than hare densities recorded during the high-phase (5 hares per ha; see Hodges 2000a).

The lower density of hares in the Rocky Mountains suggests that these populations are constrained by a different set of factors than those that limit northern populations. Northern hare populations fluctuate in broadly synchronous 8 to 11 year intervals (Smith 1983, Keith 1990, Sinclair et al. 1993; see Krebs et al. 2001a), with most estimates of amplitude between the high and low phases being 5 to 25 fold (Hodges 2000a) but sometimes approaching 100 fold (Keith and Windberg

1978, Keith 1990). Conversely, there is no quantitative evidence that spatially synchronous fluctuations occur in hare abundance across the Rocky Mountains, and the highest amplitude in yearly abundance recorded in the Rocky Mountains between observed minimum and maximum was approximately 2 fold (Wolfe et al. 1982, Koehler 1990a, b, Malloy 2000; Hodges 2000b). Several researchers have postulated that hare populations do not cycle in southern latitudes (Warren 1910, Howell 1923, Chitty and Elton 1937, Chitty 1950, Keith 1963, Dolbeer and Clark 1975, Smith 1983), but population fluctuations do occur at times in some southern areas (Green and Evans 1940a, Grange 1949, Brooks 1955, Malloy 2000). Hodges (2000b) compiled hare harvest records, hunter surveys, and indices of abundance, and concluded that hare populations in some southern areas were weakly cyclic. However, no statistical tests were performed, and it is difficult to demonstrate cyclicity when numeric variability is low and time series data sets are short in length (Berryman 2002). Therefore, the question of whether populations cycle in southern latitudes, and particularly in the central and southern Rocky Mountains, remains open-ended until hare abundance data can be gathered over the long term (i.e., spanning the period of an average northern hare cycle [8 to 11 years]). We believe that population cyclicity is an important issue to address because it has a bearing on ecological matters pertinent to southern snowshoe hare populations including metapopulation dynamics and source-sink habitat relationships.

Cause of hare population cycles

All animal populations undergo fluctuations in population size, but a true population cycle is defined as an oscillation in population numbers or density that has an obviously regular period of three or more years (Berryman 2002). The root cause of animal population cycles varies among animal species and can be broadly categorized as either exogenous or endogenous depending on whether they are caused by external variables that are themselves cyclic, or by a time-delayed feedback that suppresses survival or reproduction.

Past explanations for the snowshoe hare cycle include some exogenous mechanisms that have invariably been discounted, such as sunspots, weather, ultraviolet rays, forest fires, and natural cyclic variation in plant composition (Murray 2003 for a review of hypotheses and explanatory factors). In each case, a relationship between hare fluctuations and the exogenous factor could not be shown, but they might play some role in synchronizing hare cycles (Sinclair

Table 1. Estimates of snowshoe hare density (number of individuals/ha) based on mark-recapture and pellet count methods in portions of the southern, central, and northern Rocky Mountains. Overstory forest type, understory cover, and stand age are based on author descriptions.

Study area	Overstory forest type	Understory cover	Stand age	Field technique (pellet plot type)	Elevation (m)	Hare density (hares/ha)	Reference
Colorado	Spruce-fir	Moderate	Mature	Mark-recapture	3,210-3,480	0.10-0.90	Zahratka 2004
Colorado	Lodgepole	Open	Mature	Mark-recapture	2,850-3,100	>0.30	Zahratka 2004
Colorado	Lodgepole	Moderate to dense	?	Mark-recapture	3,100-3,415	0.73	Dolbeer and Clark 1975
Idaho	Mixed conifer	Dense	Young	Mark-recapture	1,000	0.55-0.97	Wirsing et al. 2002a
Idaho	Red-cedar, spruce-fir	Dense	Mixed	Mark-recapture	1,000	0.12	Wirsing et al. 2002a
Idaho	Lodgepole, spruce-fir	Open	Mature	Mark-recapture	1,600	0.42-0.85	Wirsing et al. 2002a
Idaho	Mixed conifer	Open to dense	Young to mature	Pellet counts (circulata)	Variable	0.12-0.23	Murray et al. 2002
Idaho	Lodgepole Mixed conifer	Moderate to dense	Young	Mark-recapture	750-900	0.76-1.34	E. Ellsworth unpublished data
Idaho	Mixed conifer	Dense	Young	Mark-recapture	750-900	0.72-0.78	E. Ellsworth unpublished data
Montana	Mixed conifer	Dense	Mature	Mark-recapture	1,450-1,700	0.10-1.45	Griffin 2004
Montana	Mixed conifer	Dense	Young	Mark-recapture	1,450-1,700	0.00-1.25	Griffin 2004
Montana	Mixed conifer	Open	Mature	Mark-recapture	1,450-1,700	0.00-0.60	Griffin 2004
Montana	Mixed conifer	Open	Young	Mark-recapture	1,450-1,700	0.46	Griffin 2004
Utah	Subalpine fir	Dense	?	Mark-recapture	2,230-2,490	0.30-2.70	Dolbeer and Clark 1975
Utah	Spruce-fir	Open to dense	Mixed	Mark-recapture	2,570	0.48	Anderson et al. 1980
Washington	Subalpine fir	Open to dense	Young	Pellet counts (rectangularb)	1,220-2,500	0.38	Quade-leu in prep.
Washington	Subalpine fir	Open to dense	Mature	Pellet counts (rectangularb)	1,220-2,500	0.21	Quade-leu in prep.
Washington	Hemlock, red-cedar, grand fir	Open to dense	Young	Pellet counts (rectangularb)	1,000-1,350	0.3	Quade-leu in prep.
Washington	Hemlock, red-cedar, grand fir	Open to dense	Mature	Pellet counts (rectangularb)	1,000-1,350		Quade-leu in prep.

^aPellet plot counts were converted to hare density via a regression derived in northern Idaho (Murray et al. 2002).

^bPellet plot counts were converted to hare density via a regression derived in the Yukon (Krebs et al. 1987, 2001b).

et al. 1993, Ranta et al. 1997, Sinclair and Gosline 1997). Similarly, some endogenous mechanisms such as induced plant defenses, disease, and parasitism are not believed to play a primary role in hare cycles. Hare herbivory can induce qualitative changes in browse plants (i.e., production of more chemical defense compounds), and it was proposed that hares might be limited by a decline in food quality when hare densities are high (Fox and Bryant 1984, Bryant et al. 1985). To test this notion, high-quality food lacking high concentrations of chemical defenses was provided to a declining hare population in Yukon, and although the hare population increased two to threefold, the hare cycle continued unchanged (Krebs et al. 1986, Sinclair et al. 1988a, Krebs et al. 1995). Thus, the conclusion is that chemical change in winter food plants is at most a contributing factor to hare cycles but not a primary cause. The role of parasites and disease has also been investigated and in both cases considered to be minor factors in hare cycles. Disease has been implicated in population die-offs (MacLulich 1937, Spalatin et al. 1966, van Nostrand 1971 cited in Dodds 1987), but such outbreaks are uncommon and there is no indication that they are cyclic. Although parasites can negatively affect hare survival and reproduction, their effects appear minor (Murray et al. 1997, 1998). Keith et al. (1985) concluded that none of the many parasites of hares caused much direct mortality. Disease and parasites may affect some hare populations sporadically (Chitty 1948, 1950), but they are not an essential cause of cycles.

Current understanding of the snowshoe hare cycle is that two endogenous mechanisms, winter food resources and specialist predators, interact to limit hare populations and cause the subsequent decline (Krebs et al. 1986, Sinclair et al. 1988a, Smith et al. 1988, Krebs et al. 1995, Hodges et al. 2001). This explanation primarily stems from the work of two long-term studies that monitored hare demography throughout a cycle. The first study, conducted in central Alberta, Canada, was largely observational. Lloyd Keith and associates (Keith 1974, 1981, Keith et al. 1984, Keith 1990) argued for a sequential interaction between food and predators whereby the decline phase is initiated by a shortage of winter food and starvation rates increase. Declining hare survival rates are exacerbated by time-delayed peaks in some predator populations (e.g., Canada lynx), and by positive functional responses of other predators that follow the increase in hare numbers. In the second, mostly experimental study, the Kluane project in Yukon, Canada (Krebs et al. 2001a), the sequential nature of the interaction was largely discounted, and food and

predators were shown to interact simultaneously. Single factor manipulations of food and predators caused a two- to three-fold increase in the abundance of hares whereas a treatment plot with addition of food and reduction of predators resulted in hare populations that were >10 times the densities of controls (Krebs et al. 1995, Hodges et al. 2001). Decreased survival during the decline phase appears to be the result of increased predation. However, it remains unclear why reproductive output is also low during this phase. Hik (1994, 1995) proposed that the amount of food available to hares might be restricted when predation-risk is high because hares avoid high-risk areas in favor of increased cover. In doing so, hares might voluntarily select habitats with poorer food resources, are in poorer condition, and experience reduced productivity. It was further proposed that hares experience physiological stress when predation risk is high (or perhaps when food resources are low), resulting in decreased reproductive output and extended maternal effects (Boonstra and Singleton 1993, Boonstra et al. 1998a, b). Presently, hypotheses that incorporate hare behaviors and stress physiology remain tentative.

Why do hare populations in the Rocky Mountains lack large-amplitude cycles?

Habitat patchiness, an abundant and diverse assemblage of generalist predators, and an interaction between these two factors are the most likely explanations for why snowshoe hare cycles are suppressed in the Rocky Mountains and other areas south of the boreal forest. Here, we briefly discuss supporting theory and evidence for each hypothesis.

Early hare researchers noted that abundant populations were often widely separated and lacked apparent connectivity, and the argument was made that the patchy distribution of hare habitat might explain the lack of snowshoe hare cycles south of the boreal forest (Warren 1910, Howell 1923, Chitty and Elton 1937). In support of this notion, current metapopulation and source/sink theory suggests that disparate and demographically independent subpopulations are unlikely to have synchronous cycles (Pulliam 1988, Hanski 1999). Also, there is some empirical evidence in non-cyclic populations that demographic rates vary among subpopulations (Keith et al. 1993, Wirsing et al. 2002a, Griffin 2004). For instance, demographic rates in Montana strongly differed among patches with distinct habitat attributes (i.e., mature versus young and closed versus open; Griffin 2004). Unfortunately, no measure of the relative connectivity among subpopulations

or across the landscape has yet been made, although genetic differentiation between hares in Montana and in boreal forests was large (Burton et al. 2002).

Patchy habitat distribution in more southern forests has also been hypothesized to suppress hare cycles via an interaction with the abundant and diverse guild of generalist predators that exist there (Dolbeer and Clark 1975, Wolff 1980, 1981, and Buehler and Keith 1982, Keith et al. 1993, Wirsing et al. 2002a). Two possible scenarios that have been supported experimentally are that 1) habitat patches provide some degree of safety, but dispersing hares are heavily preyed upon by facultative predators and thus are unable to establish themselves in sub-optimal habitat (i.e., the refugium model; Wolff 1980, 1981, Sievert and Keith 1985), and 2) hare populations are suppressed by intense predation within habitat patches (Keith et al. 1993, Wirsing et al. 2002a). In either case, the argument could be made that generalist predators prevent hare populations from increasing within a patchy environment. However, it has not been verified that southern hare populations are really subject to higher and more consistent predation rates than northern hare populations. We suggest that there is currently not enough empirical support for the refugium model, and the possibility that generalist predators could prevent hare cycles irrespective of patchiness has not been sufficiently evaluated.

In theory, generalist predators are believed to have a stabilizing influence on prey populations because they do not rely on one prey species and can “switch” to alternative prey when one prey becomes scarce. Conversely, specialist predators are believed to be instrumental in maintaining population cycles (Andersson and Erlinge 1977, Korpimäki et al. 1991, Hanski et al. 2001). Perhaps the best-studied example of such a relationship is in Fennoscandia, where there is a latitudinal gradient in microtine rodent cyclicity that is attributed, at least in part, to changes in the number of generalist (and nomadic) predators (Hanski et al. 2001; but see Oksanen et al. 2001). A similar scenario might exist in North American hare populations, where a shift in population dynamics with latitude corresponds to an apparent increase in the abundance and diversity of generalist predators. For instance, within the Rocky Mountains, hares are preyed upon by several generalist species including coyote (*Canis latrans*), bobcat (*Lynx rufus*), fisher (*Martes pennanti*), marten (*Martes americana*), barred owl (*Strix varia*), great-horned owl (*Bubo virginianus*), northern goshawk (*Accipiter gentilis*), and red-tailed hawk (*Buteo jamaicensis*). In comparison, the boreal forest predator guild is smaller and dominated by Canada lynx as the prototypical hare

specialist. Simple regional comparative analyses in prey diversity are, however, confounded by the fact that the guild of predators that occupies a particular site can differ widely across the Rocky Mountains. Moreover, the importance of hares in the diet of predators is virtually unknown within deep snow environments where alternative prey are largely unavailable, and generalists may actually be obligate hare predators during the winter, much as they are in boreal forests (e.g., great-horned owl and coyote; O'Donoghue et al. 1998, 2001). The challenge, then, is to develop a much more robust understanding of predator/prey interactions in southern hare populations before comparative analyses can be made.

Breeding biology

The breeding season of snowshoe hares begins in late winter (January – April) and ends in late summer to early fall (July – October), during which time a single female can have up to four litters. Hares are polygamous (Burton 2002), and both sexes begin mating in their first spring, but rarely in their first summer (Keith and Meslow 1967, Vaughan and Keith 1980). Males attempt to mate with several females, and mating may occur within 24 hours post-partum (O'Donoghue and Boutin 1995). Gestation period ranges from 34 to 40 days, and females exhibit immediate post-partum breeding behavior (Sevaraid 1945, Meslow and Keith 1971, Bittner and Rongstad 1982). Females within a population have synchronous birth periods; therefore, distinct litter groups can be distinguished. The onset and cessation of male breeding condition is largely controlled by photoperiod (Sevaraid 1945, Davis and Meyer 1972, 1973a, b). In most areas, the mean date of the birth of the first litter ranges from mid-March to late April, with some variation accounted for by a delay in breeding at higher latitudes (Murray 2000, Murray 2003). However, first litter production is delayed in the western United States despite the more southern latitude. In Colorado, first litters were conceived from late April to early May (Dolbeer and Clark 1975), mid-April in Utah (Dolbeer and Clark 1975), mid-May to early June in Idaho (A. Wirsing, personal communication 2002, E. Ellsworth unpublished data), mid to late May in Oregon (Black 1965), and late March to early April in Montana (Adams 1959). It is postulated that hares at higher elevations might delay the onset of breeding (Keith 1966, Murray 2000) to coincide with more optimum environmental breeding conditions. There also is some evidence that poor winter nutrition can delay the onset of reproduction (Vaughan and Keith 1981), but the timing of first litter production did not differ between food supplemented and non-supplemented hares (Ellsworth

and Murray in prep. a), indicating that poor food quality was not a proximate mechanism for late breeding in this Idaho population.

Neonate and juvenile development

Like other species of *Lepus*, newborn snowshoe hares (leverets) are precocial, fully furred, and can open their eyes within an hour after birth (Severaid 1942). Birth weight is variable among populations and ranges from an average of 40 g in Montana (Adams 1959) to 82 g in New York (Dell and Schierbaum 1974), with intermediate averages of 67 g in Maine (Severaid 1942) and 59 to 62 g in Yukon (Graf and Sinclair 1987, O'Donoghue and Krebs 1992). Leverets are usually nursed once a day soon after sunset for 25 to 28 days, but young from the last litter of the season may nurse for up to 2 months (Severaid 1942, Rongstad and Tester 1971, Graf and Sinclair 1987, O'Donoghue and Bergman 1992). Within 1 to 4 days after birth, young move apart from one another and leverets, spend much of the day alone in hiding cover but within their mother's home range (O'Donoghue and Bergman 1992). The behavior of nursing females and their offspring is apparently well-adapted to minimizing predation risk. Hares have highly concentrated milk (Martinet and Demarne 1984), which allows them to nurse for short, infrequent periods, thus minimizing the amount of time the whole litter is in one place (O'Donoghue and Bergman 1992).

During the first 60 days following birth, juveniles develop at a rate of 16 to 17 g per day (Severaid 1942, Graf and Sinclair 1987) and typically attain adult body weight 9 to 11 months following birth (Keith and Windberg 1978). Leveret home range size increases rapidly and reaches the size of an adult female within 8 weeks of age (Rongstad and Tester 1971, O'Donoghue and Bergman 1992). Interestingly, juvenile growth rate does not appear to be a function of food availability during the summer, as supplementation did not increase juvenile growth rates (O'Donoghue and Krebs 1992, Boonstra et al. 1998a). In cyclic populations, juvenile growth may instead be linked to maternal condition, which in turn is partly a function of the phase of the population cycle (Boonstra et al. 1998a, b, Sinclair et al. 2003).

Causes of death

The fate of leverets has been reported only from the Yukon (O'Donoghue 1994, Hodges et al. 2001) and northern Idaho (Wirsing 2001). In the Yukon, neonate mortality was high particularly during the first 5 days after birth and was primarily the result of predation,

although some hares did die of abandonment or exposure (O'Donoghue 1994, Hodges et al. 2001). Leverets were most often killed by red squirrels (*Tamiasciurus hudsonicus*), but also by arctic ground squirrels (*Spermophilus parryii*), short-tailed weasels (*Mustela erminea*), and raptors of variable sizes, including boreal owls (*Aegolius funereus*), great-horned owls, red-tailed hawks, northern goshawks, and American kestrels (*Falco sparverius*; O'Donoghue 1994, Stefan 1998, Hodges et al. 2001). Although it appears likely that leverets in the Rocky Mountains incur similar losses, no mortality of 2 to 6 week-old leverets ($n = 12$) was observed in northern Idaho (Wirsing 2001).

In northern populations, predators are the proximate cause of post-weaned snowshoe hare mortality 58 to 100 percent of the time (Brand et al. 1975, Keith et al. 1984, Boutin et al. 1986, O'Donoghue 1994, Murray et al. 1997, Ferron et al. 1998, Gillis 1998, Hodges et al. 2001). Percent predator mortality tends to be highest during the low-phase (Hodges et al. 2001) while high rates of non-predation mortalities (mainly starvation) are common only when food is limited during the spring and winter of cyclic highs and the subsequent decline (Keith et al. 1984, Boutin et al. 1986, Hodges et al. 2001). In southern populations, predators account for 80 to 100 percent of hare mortalities (Sievert and Keith 1985, Fies 1993, Keith et al. 1993, Cox et al. 1997, Wirsing et al. 2002a, Abele 2004, Bull et al. 2005, Ellsworth and Murray in prep. b). Among only those studies conducted in the western United States, predators accounted for 93 percent and 80 percent of mortalities in Idaho (Wirsing et al. 2002a, Ellsworth and Murray in prep. b, respectively), and 98 percent of mortalities in two Oregon studies (Abele 2004, Bull et al. 2005).

Post-weaned hares are at risk from a suite of larger mammalian predators and raptors, including, but not limited to, bobcat, lynx, red fox (*Vulpes vulpes*), gray wolves (*Canis lupus*), fisher, American marten, mink (*Mustela vison*), wolverine (*Gulo gulo*), mountain lion (*Felis concolor*), northern goshawk, red-tailed hawk, golden eagle (*Aquila chrysaetos*), northern hawk-owl (*Sirnia ulula*), great-grey owl (*Strix nebulosa*), great-horned owl, barred owl, and the common raven (*Corax corax*; Adams 1959, Earhart and Johnson 1970, Rausch and Pearson 1972, Keith et al. 1977, Raine 1987, Kuehn 1989, Keith 1990, Poole and Graf 1996, O'Donoghue et al. 1997, Stenseth et al. 1997, McIntyre and Adams 1999, Hodges et al. 2001, Wirsing et al. 2002b, E. Ellsworth unpublished data). Terrestrial predators hunting hares are successful = 30 percent of the time (Raine 1987, Murray et al. 1995, O'Donoghue et al. 1998).

Hares also succumb at much lower rates to disease, infections, ulcers, and possibly nutritional deficiencies, as well as human-related mortality including “trap-sickness”, hunting, and automobile accidents. Although parasites rarely kill hares, there is some evidence that endoparasites may weaken hares and increase their vulnerability to predation (Keith et al. 1986, Murray et al. 1997). Population die-offs also have resulted from bacterial epidemics of *Staphylococcus aureus*, species of the bacterium *Clamydia*, and the bacterium *Pasteurella tularensis*, which causes tularemia (MacLulich 1937, Spalatin et al. 1966, van Nostrand 1971 cited in Dodds 1987). See Murray (2003) for a more thorough review of hare parasites and infectious diseases. Another apparent cause of hare die-offs is opisthotonic shock disease, which was first described in Minnesota (Green and Larson 1937, 1938, Green et al. 1938). However, it is difficult to distinguish “shock disease” from starvation because malnourished hares have similar symptoms (e.g., low body mass, depressed levels of blood sugar and liver glycogen; Keith et al. 1968, Iversen 1972, Keith et al. 1984). In Idaho, 25 hares over three years died of an unknown condition during a two week period in late spring (late May – early June), and the epidemiology of the ailment is consistent with grass tetany (hypomagnesemia), a seasonal malady identified in ungulates (Jefferson et al. 2001, C. Robbins personal communication 2003). Historically, hunting has probably been the greatest single source of human caused mortality in hares, but currently it is not believed to be a significant cause of death in most areas (Hodges 2000a). Hares also are killed by automobiles, but rates are low (Wirsing et al. 2002a, E. Ellsworth unpublished data).

Movement patterns

Snowshoe hares forage and engage in social behavior primarily between dusk and dawn; they are relatively inactive during the day when they occupy areas of dense vegetation (Keith 1964, Mech et al. 1966, Foresman and Pearson 1999, Abele 2004). Although this 24-hour activity pattern holds true for hares in most areas and in most seasons, hares are active during daylight during the summer at higher latitudes (Keith 1964, Boulanger and Krebs 1994, Hodges 1998). Hares also are sensitive to moonlight and adjust their movement patterns when illumination is intense, apparently to reduce predation risk particularly when the ground is snow-covered (Gilbert and Boutin 1991, Griffin et al. 2006).

Some seasonal differences in activity have been recorded, with activity levels being highest in the

spring and summer, moderate in the fall, and lowest in the winter (Abele 2004). Increased spring activity levels coincide with breeding activity and improved food resources. Social interactions during the breeding season have rarely been observed in free-living snowshoe hares, but observations of captive animals suggest that courtship and aggressive behaviors may be extensive at this time (Bookhout 1965a, Ferron 1993). Outside of the breeding season, there is little evidence to suggest that hares engage in many social interactions, and most activity is likely limited to foraging.

Natal dispersal of young hares can begin soon after weaning, as early as 1 month of age (O'Donoghue and Bergman 1992, Gillis 1997), and thereafter hares of all ages are known to disperse. Determining what constitutes a dispersal movement is sometimes difficult, however, because some hares make long-distance movements on a regular basis without necessarily vacating their home range (Hodges 2000a). Hares may disperse as far as 20 km, but generally they disperse much shorter distances (Aldous 1937, O'Farrell 1965, Keith et al. 1993, Hodges 1998, Gillis and Krebs 1999). In the western United States, 90 percent of hares in Montana moved less than <1.8 km (Griffin 2004), and the average dispersal distances of hares in Idaho was 1.6 km (E. Ellsworth unpublished data).

Males and females, as well as hares of different age classes, disperse throughout the year, with pulses often occurring in the spring and autumn (Murray 2003). However, Griffin (2004) found greater maximum movement distances in the fall than in any other season while Boutin et al. (1985) found that the highest dispersal rates occurred in the winter during the cyclic high-phase. Mammalian natal dispersal is predominantly biased towards males (Greenwood 1980), but there is no apparent sex bias in hare dispersal rates in most hare populations (Windberg and Keith 1976, Keith et al. 1984, Boutin et al. 1985, O'Donoghue and Krebs 1992, Keith et al. 1993, Burton et al. 2002). Dispersal rates have been shown to vary by age class, with juveniles tending to disperse at a higher rate than adults (Dolbeer and Clark 1975, Windberg and Keith 1976, Keith et al. 1984, Boutin et al. 1985, Keith et al. 1993).

In the western United States, barriers to hare dispersal include unforested areas, steep slopes, rocky and rough terrain, fast-moving rivers (although hares are known to swim), and urban areas. It is not known how far hares will move across open areas, but some forested patches and even entire mountain ranges, such as the Bighorn Mountains, may effectively be habitat

“islands” surrounded by uninhabitable areas. Potential dispersal corridors include areas with vegetative structure, such as riparian corridors, dense shrublands, or patches of woodlands in close proximity to one another. Hares that occupy treeless subarctic ecosystems are generally restricted to riparian zones with abundant shrub cover (St.-Georges et al. 1995). Hares will use small clearcuts for travel or feeding if forested stands are nearby (Conroy et al. 1979, Monthey 1986, Scott and Yahner 1989, Thomas et al. 1997).

Habitat

Home range

The home range size of snowshoe hares has been measured several times, and average estimates range from approximately 5 to 10 ha (Keith 1990, Hodges 2000a, Murray 2003). However, the two primary methods used to measure home range size in the field, live-trapping and radio-telemetry, tend to generate different results, and this hinders comparative analyses. Hodges (2000a) emphasizes the need for standardizing methods.

Snowshoe hares are non-migratory and generally occupy the same area throughout the year. Hares in some populations may either make short-distance seasonal movements between winter and summer foraging areas, or show pronounced seasonal habitat use patterns (Adams 1959, Bookhout 1965b, c, Wolff 1980, Wolfe et al. 1982). Areas occupied by hares often overlap extensively with conspecifics. There is no evidence that hares defend territories, and intraspecific aggression apparently does not influence home range size (Boutin 1980, Boutin 1984b).

A review of home range size found that males tend to have slightly larger year-round ranges than females (averaging 6.7 and 5.2 ha, respectively; Keith 1990), but other studies did not find sex differences in home range size (O’Farrell 1965, Dolbeer and Clark 1975). Home range size differences tend to be most pronounced during the breeding season, probably because males move more in order to mate with several females (Hodges 1999). Adult females with young have smaller home ranges during the spring and summer (Bider 1961, Graf and Sinclair 1987, O’Donoghue and Bergman 1992, Allcock 1994, Jekielek 1996) while males move farther abroad when females are in oestrous (Bider 1961, Chu 1996).

Home range size may be influenced by ecological factors such as population density, per capita food

resources, habitat quality (e.g., availability of understory cover), and predation risk (Murray 2003). As expected, home range size appears to be inversely related to population density. Food supplementation has sometimes resulted in reduced home range size but has had no effect in other cases (Boutin 1984a, Hodges 1999). Keith et al. (1993) failed to detect a relationship between hare home range size and habitat quality. Another ecological factor that may influence home range size is predation risk. Hodges (1999) reported a positive relationship between predation risk and hare home range size. This was an unexpected result given that prey animals are expected to decrease their movements when risk is high, and Hodges (1999) suggested that hares might be better able to evade predators by moving more rather than less, or vacating areas quickly when they encounter predator sign.

Habitat use

Although there are some exceptions, snowshoe hares primarily occupy dense, thick woodlands in environments with relatively deep winter snow accumulation (**Figure 4**). This is true regardless of the forest type that hares occupy, including boreal forests, aspen parkland, conifer forests, deciduous woodlands, orchards, tree plantations, and riparian woodlands (Adams 1959, Wolff 1980, Wolfe et al. 1982, Pietz and Tester 1983, Carreker 1985, Litvaitis et al. 1985a, MacCracken et al. 1988, Ferron and Ouellette 1992, Hodges 2000a, Wirsing et al. 2002a, Murray 2003, Zimmer 2004). Optimum densities of woody shrubs and small trees range from 4,600 to 33,210 stems per ha (Brocke 1975, Wolff 1980, Parker 1984, Litvaitis et al. 1985a, Monthey 1986, Parker 1986, Koehler 1990a, Griffin 2004) and vary with habitat type and stand age. Extremely dense stands (>40,000 stems per ha) may be of little use to hares if understory cover and browse are sparse (Adams 1959, Litvaitis et al. 1985a). Forests with open understories also lack thermal and hiding cover (Brocke 1975, Koehler 1990b). Non-forested areas are usually avoided, as are stands comprised of seedlings and more mature forests that have little undergrowth (Gashwiler 1959, Pietz and Tester 1983, Murray et al. 1994, St.-Georges et al. 1995). In the winter, areas with less than 40 percent vegetation cover at or near snow level were unacceptable to snowshoe hares (Wolfe et al. 1982). With the notable exception of coastal forests of the Pacific Northwest (Black 1965, Mozejko 1971), there are relatively few hare populations that exist where snow cover does not persist for several months.

A dense understory provides hares with protection from predators, thermal protection, and winter food



Figure 4. Snowshoe hare habitat and tracks in a mixed-conifer forest in northern Idaho.

(Belovsky 1984, Sievert and Keith 1985, Barta et al. 1989, Rohner and Krebs 1996, Wirsing et al. 2002a). Of these, Murray (2003) argues that refuge from predators is the most important factor driving selection. Hares are able to subsist on a wide variety of plant species, and there is some evidence that they select areas of dense cover regardless of plant species composition (Wolff 1980, O'Donoghue 1983, Litvaitis et al. 1985a, Parker 1986, Rogowitz 1988, Ferron and Ouellette 1992, Thomas et al. 1997). Hares also change habitats, movements, and diets in response to predation risk (Hik 1994, 1995, Boonstra et al. 1998b, Morris 2005), and they are known to vacate thinned forests despite an obvious abundance of food, apparently because hiding cover is reduced (Abele 2004). However, the notion that habitat selection is driven by predator avoidance was not supported by results from Hodges and Sinclair (2005), who found that browse site selection reflected browse availability rather than predator avoidance. Moreover, food resources may be inadequate in some dense habitats, and in these circumstances hares might forage in areas separate from where they take cover (Orr and Dodds 1982, Ferron and Ouellette 1992, Hik 1995). This pattern was apparent in northern Idaho where hares resided during the day in dense stands of western red-cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) that were rarely consumed and of poor nutritional value, but they foraged in more open stands of lodgepole pine (*Pinus contorta*), which is a relatively nutritious browse (E. Ellsworth unpublished data). Adams (1959) found that hares avoided feeding in very dense stands and suggested that shade interfered with the growth of plants preferred by hares. In areas where cover and food are not positively correlated, a

key component of habitat selection and quality might be the proximity of dense cover to quality forage. The affinity of hares for edge habitat in some places supports this notion (Conroy et al. 1979, Pietz and Tester 1983, Scott and Yahner 1989).

Snowshoe hares in the western United States occur in forests dominated by aspen (*Populus tremuloides*), bristlecone pine (*Pinus longaeva*), cottonwood/willow (*Populus* sp./ *Salix* sp.), Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce/subalpine fir (*Picea engelmannii*/*Abies lasiocarpa*), Gambel oak (*Quercus gambelii*), grand fir (*A. grandis*), limber pine (*Pinus flexilis*), lodgepole pine, western hemlock/ western red cedar, western larch (*Larix occidentalis*), and white fir (*A. concolor*; Hodges 2000b, Bartmann and Byrne 2001). However, because grand fir, western hemlock, western red cedar, and western larch do not occur in Colorado and Wyoming, they are not discussed further. Moreover, there is little evidence that hares in the central and southern Rocky Mountains are strongly associated with some of these species such as aspen (Miller 2005). Therefore, we focus our attention on two habitat types where the most abundant hare populations are often reported: Engelmann spruce/subalpine fir and lodgepole pine forests (Clark 1973, Dolbeer and Clark 1975, Winn 1976, Koehler 1990a, Thomas et al. 1997, Malloy 2000, McKelvey and McDaniel 2001, Zahratka 2004, Zimmer 2004, Miller 2005, Quade-Leu in prep.). Hares prefer lodgepole pine at least in part because it is a nutritious winter food (Wirsing and Murray 2002, Ellsworth and Murray in prep. a), and the cover attributes of many spruce-fir and young lodgepole forests are suitable. In addition, accumulation of deep

winter snow within these mid- to high-elevation forests may serve as a refuge for hares because some predators (e.g., bobcat) avoid areas with deep snow, where they are at a disadvantage (Koehler and Hornocker 1989).

Hares do not use all spruce-fir and lodgepole pine forests equally, however, and there are conflicting reports of the importance of these forest types to hares. In some places, hare and lynx are more abundant in lodgepole pine than in spruce-fir forests (Koehler et al. 1979, 1990a, and see McKelvey et al. 2000b). On the other hand, in the Southern Rocky Mountains, hares have been found to be more abundant in mid- to late-seral stages of spruce-fir forests than in lodgepole pine forests (Zahratka 2004, Miller 2005). It is unclear, however, to what degree this is due to habitat preference, or to the fact that much lodgepole pine in the Southern Rocky Mountains is in a mature state and, as such, is poor habitat for snowshoe hares. Engelmann spruce and especially subalpine fir often retain their lower branches, providing effective shelter for hares (**Figure 5**), and old gap-phase spruce-fir forests often have a dense understory of young trees. Buskirk et al. (2000) suggested that hare abundance in mesic forests, including subalpine fir, have bimodal peaks that correspond to increased sapling density during both early and late stages of spruce-fir forest succession.

Conversely, optimum structural characteristics of a lodgepole pine forest are temporally restricted to a period when trees are young (**Figure 6**). Lodgepole pine is a post-fire species, and a typical pattern following a burn is for serotinous cones to release large quantities of seeds that produce a dense, even-age stand. After a fire, hare populations can be quite

low for several years (e.g., Yellowstone National Park; K. Hodges personal communication 2005, C. Robbins personal communication 2003), but hare abundance increases along with sequential structural changes in horizontal cover and winter food availability. Within a comparatively short timeframe post-disturbance, lodgepole pine begins to self-prune, and thereafter branches are too high to be useful to hares as either food or cover.

Hare densities are low to moderate from the initial seedling phase of lodgepole pine regeneration to sapling stage, highest while trees are small to mid-sized, and low again in pole-sized and mature forests that are self-pruned and retain few lower branches (Koehler et al. 1979, 1990a, Malloy 2000, Zimmer 2004, Miller 2005). Stands comprised of mid-sized trees are preferred to other stands because understory cover can be extensive and hares are able to reach live lodgepole branches to feed. The necessary combination of winter food and cover is lacking in very young and mature stands (Koehler et al. 1990a, b, Wirsing and Murray 2002, Zimmer 2004). Younger lodgepole pine forests can provide an abundant source of food, and hare use can be high if stands are dense (Sullivan 1984, McKelvey and McDaniel 2001). However, hares avoid areas where stem density is low and deep snow buries all but the tops of saplings. The time frame that it takes hare populations to become re-established in lodgepole pine forests after disturbance is probably associated closely with the regenerative capacity of the landscape, which is influenced by topographic relief, moisture, and mineral and organic content of the soil (Baumgartner et al. 1984, Koch 1996).



Figure 5. Snowshoe hare habitat in a forest dominated by subalpine fir.

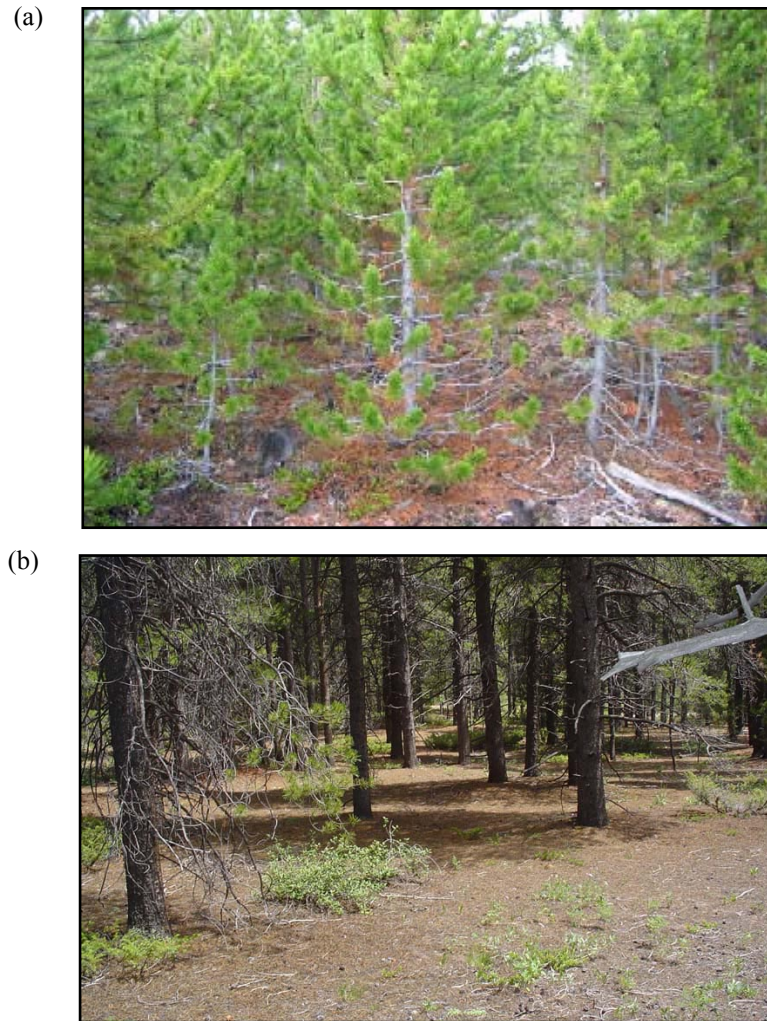


Figure 6. Large differences in understory cover that often exist between regenerating (a) and mature (b) lodgepole pine forests.

There is some support for age-related differences in hare abundance, as high hare densities correlated with younger stands in relatively moist forests in northeastern Washington (20 and 25 to 55 years old, respectively; Koehler 1990b, Quade-Leu in prep.), and slightly older stands in drier sites in Montana (67 and 50 to 60 years old, respectively; Koehler et al. 1979, Zimmer 2004). In Colorado, Miller (2005) found that hare abundance was low in stands of small diameter trees (2.54 to 12.69 cm) that were apparently less than 25 years old, and higher in stands with medium-sized trees (22.9 to 40.6 cm). Although the association between hares and lodgepole pine has not been compared among different successional communities, we believe that the high variability in structure and community role that lodgepole pine shows across its range (Pfister and Daubenmire 1973, Volland 1984, Koch 1996) could have a bearing on hare abundance patterns.

Food habits and nutritional ecology

Morphology and physiology of digestion

Snowshoe hares possess enzymes that enable them to readily digest plant cell solubles. Similar to other herbivores that consume coarse vegetation, hares also rely on microbial digestion in order to use structural carbohydrates in food. Hares are hind-gut fermenters; bacterial fermentation takes place in the sack-like cecum that is located at the juncture of the large and small intestine (Snipe 1978 for a description of rabbit digestive anatomy). End products of microbial digestion include volatile fatty acids, which are mainly absorbed through the cecal wall, and protein and minerals, which are excreted in soft cecal pellets (cecotropes) and eaten directly from the anus (Bjornhag 1994). Cecotropes in a similar hare species, *Lepus timidus*, have been

shown to be high in crude protein and contain high concentrations of other minerals such as potassium, phosphorus, magnesium, and sodium (Pehrson 1983). Rabbits (*Oryctolagus cuniculus*) prevented from eating their cecotropes lost considerable amounts of protein, vitamins, and electrolytes, illustrating the importance of cecotrophy (Bjornhag 1994).

Food requirements

Animal food requirements are determined by the amount of energy they expend and the amount of energy and other nutrients that they can extract from their diet (McNab 2002). During the late winter, the field metabolic rate (FMR) of free-living snowshoe was about 740 kilojoules (kJ) per kg per day, and based on conifer energy concentrations and digestibility, it was estimated that hares needed to consume approximately 230 g wet matter (WM) per kg per day, or about 25 percent of their body mass, to meet this energy demand (Ellsworth and Murray in prep. c). Snowshoe hares in Michigan and Alberta consumed similar amounts of natural winter food on a mass-specific basis (~ 219 and 234 g WM per kg per day, respectively; Bookhout 1965, Pease et al. 1979, respectively); however these studies were done in captivity, and intake requirements of free-living hares are expected to be elevated because free-living hares use about 15 percent more energy than captive hares in the same thermal environment (Ellsworth and Murray in prep. c).

No studies have directly measured the consumption rates or FMR of free-living hares during the summer, but based on captive experiments, summertime energy requirements were approximately 110 kilocalories (kcal) per kg^{0.75} per day (Holter 1974), which is substantially less than estimated digestible energy intake of free-living hares during the winter (203 kcal per kg per day; Ellsworth and Murray in prep. c). Summer food requirements of reproductive hares are likely to be elevated, but energy costs have not been examined. Moreover, one study found that captive hares had a higher basal metabolic rate (BMR) and required greater caloric intake in the summer than winter (Hart et al. 1965). Apparently, hares were able to offset the increased thermoregulatory demands of winter with fur insulation and low heat conductance (Hart et al. 1965), and they might use a depressed winter BMR as an energy saving strategy (Thomas 1987). Based on energy requirements and constraints for feeding time, digestive capacity, and sodium requirements, Belovsky (1984) developed an optimal foraging model and

calculated that hares weighing 1.35 kg consumed about 241 g per day in the summer and 203 g per day in the winter. The nature of seasonal differences in hare food and energy requirements remains uncertain given that summer FMR and food intake have not been examined in free-living hares.

Patterns of forage selection

Regional differences exist in the diet of snowshoe hares across North America (Hodges 2000b, Murray 2003 for a review), but almost all hares eat woody browse in the winter and more herbaceous foods in the summer. Accordingly, winter dietary breadth is substantially lower than summer. There is no evidence that hare populations are limited by summer food abundance, but the abundance of winter food resources can fall below requirements (Pease et al. 1979, Wirsing et al. in prep.) and limit the growth of cyclic hare populations (Keith et al. 1984, Krebs et al. 1995). Moreover, food quality is often more important than quantity, particularly in heavily browsed areas, because woody browse contains low protein and low energy, as well as secondary defense chemicals designed to deter herbivory (Bryant 1981, Sinclair et al. 1988b, Jogia et al. 1989, Reichardt et al. 1990a, b).

Hares show strong selection for certain plants, a foraging strategy that may maximize energy and protein, and minimize fiber and secondary compound consumption. Belovsky (1984) suggested that plant sodium concentrations could also be limited in some environments and influence forage selection. Hares increase their protein intake by selecting relatively protein-rich plant parts such as buds or small diameter twigs (≤ 4 mm; Pease et al. 1979, Wolff 1980, Bryant 1981, Fox and Bryant 1984, Hodges 2000b), avoid plants with potent chemical defenses (Bryant and Kuropat 1980, Bryant et al. 1985, Rodgers and Sinclair 1997), and select plant species and age classes with high protein, high energy, or low fiber concentrations (Klein 1977, Sinclair et al. 1982, Sinclair and Smith 1984, Rogowitz 1988, Sinclair et al. 1988a, Schmitz 1992, Rangen et al. 1994, Nams et al. 1996, Rodgers and Sinclair 1997, Seccombe-Hett 1999, Wirsing and Murray 2002, Hodges and Sinclair 2003, Ellsworth and Murray in prep. b). However, there have been some inconsistent selection patterns among studies concerning the role of protein or energy, which may reflect either regional differences in plant composition or in environmental conditions that affect nutritional demands (Ellsworth and Murray in prep b).

Winter food habits in mountainous areas of western North America

In western mountains, snowshoe hares mainly consume conifer trees (**Figure 7**) during the winter, including subalpine fir, grand fir, western larch, Engelmann spruce, lodgepole pine, western white pine, ponderosa pine, Douglas-fir, western red-cedar, and western hemlock (Adams 1959, Wirsing and Murray 2002, Zahratka 2004, Zimmer 2004, Ellsworth and Murray in prep. b). Angiosperm shrubs and trees are also consumed, including Saskatoon serviceberry (*Amelanchier alnifolia*), creeping barberry (*Mahonia repens*), ceanothus (*Ceanothus* sp.), mountain boxwood (*Paxistima myrsinites*), rose (*Rosa* sp.), thimbleberry (*Rubus parviflora*), Canada buffaloberry (*Shepherdia canadensis*), and blueberry (*Vaccinium* sp.) (Adams 1959, Thomas et al. 1997, A. Wirsing personal communication 2002, E. Ellsworth unpublished data). However, the availability of shrubs and small trees depends on snow accumulation, which can vary in the Rocky Mountains temporally and spatially.

At lower elevations, or in areas with less snow cover, there is some indication that shrubs and even herbaceous plants are more major winter diet items (Adams 1959, Mozekjko 1971, Thomas et al. 1997). At a local scale, food availability is affected by factors that influence snow accumulation and persistence, such as canopy closure, forest structure, or topographical aspect. For example, on open south-facing slopes in northern Idaho, hares are able to access highly preferred

shrubs such as *Vaccinium* sp. much earlier in the spring than they can in shaded forests or on north-facing slopes (E. Ellsworth personal observation). Snow accumulation also can have a dynamic effect on total winter plant availability. Hares can only reach forage up to ~50 cm above the ground or snow surface (Pease et al. 1979); therefore, changing winter snow levels can provide access to tree branches at different heights (Keith et al. 1984, Wirsing and Murray 2002, Ellsworth and Murray in prep. b). The influence of deep snow on feeding patterns was observed in northern Idaho (Wirsing and Murray 2002, Ellsworth and Murray in prep. b), eastern Washington (Koehler 1990a, b), southern Montana (Zimmer 2004), southwestern Colorado (Zahratka 2004), British Columbia (Sullivan and Sullivan 1982, Sullivan 1984), and Alberta (Johnstone 1981, Ives and Rentz 1993).

The predominance of conifers in the diet of hares has some potentially negative nutritional implications because conifers are generally believed to be substandard forage for most herbivores (Bryant et al. 1992a, b), and hares avoid them in many areas (Bookhout 1965b, Klein 1977, Bryant and Kuropat 1980, Bryant 1981, Bryant et al. 1991). However, in northern Idaho there was no indication that free-living hares subsisting on a winter diet of conifers were in worse winter condition or had reduced fitness compared to hares provided with high-protein rabbit chow (Ellsworth and Murray in prep. a). In fact, digestible protein values were higher in some Idaho conifer species than in shrubs consumed by hares in boreal forests (Ellsworth 2004), and there was some



Figure 7. A lodgepole pine twig browsed by snowshoe hare.

evidence that secondary defense compounds in Idaho conifers were not potent (Wirsing and Murray 2002). Diet preference and nutritional benefits are not equal among Rocky Mountain conifer species, however, and captive hares selected those species with high protein content (Wirsing and Murray 2002) and high digestible protein (**Figure 8**; Ellsworth and Murray in prep. b). Digestible protein of the most preferred species, lodgepole pine, was the only species that exceeded the minimum digestible protein requirements of hares (Holter et al. 1974; Ellsworth 2004). Not surprisingly, lodgepole pine was the most heavily browsed conifer species by free-living hares in Idaho (Ellsworth and Murray in prep. b), and it comprises a large proportion of hare's diet in other areas, ranging from 3 to 18 percent in northeastern Washington (Quade-Leu in prep.), 59 percent in southern Montana (Zimmer 2004), and as high as 96 percent in north-central Washington (Koehler 1990). Moreover, in British Columbia (Sullivan and Sullivan 1982, Sullivan 1984) and Alberta (Johnstone 1981, Ives and Rentz 1993) hares forage extensively on lodgepole pine and are regarded as silvicultural pests (Koch 1996). No other conifer in the Rocky Mountains is consistently as important as a winter food item, and the relative nutritional value of lodgepole pine could be an important reason why hares prefer young lodgepole pine stands. Food trials with other conifers indicate that hares were able to maintain weight for at least 6 days while consuming Douglas-fir, lodgepole pine, western white pine, and ponderosa pine, but they lost body mass during trials with Engelmann spruce (~ 4

percent), subalpine fir (~ 8 percent) western hemlock (~ 8 percent), western larch (~ 9 percent), western red cedar (~ 6 percent), and grand fir (~ 9 percent; Ellsworth and Murray in prep. b). However, nutritional content in plants tends to vary regionally and locally, and it is preliminary to suggest that low-quality conifers in northern Idaho are avoided in other environments. For example, in Colorado and Wyoming hares may feed heavily on subalpine fir, or white bark pine in Wyoming (Zahartka 2004, E. Ellsworth personal observation).

Summer food habits in western North America

Similar to their summer food habitats in other regions, snowshoe hares primarily consume grasses, sedges, forbs, and leaves of some woody plants in the western United States. In Montana, hares consumed grasses (*Calamagrostis rubescens*, *Koeleria cristata*), forbs (*Balsamorhiza* spp., *Erythronium grandiflorum*, *Arnica* spp, *Fragaria* spp., *Smilacina* spp., *Taraxacum* spp, *Collinsia* spp., *Claytonia* spp.), and leaves of shrubs (*Spirea betulifolia*, *Arctostaphylos uva-ursi*; Adams 1959). In western Oregon, hares ate large amounts of forbs (*Lupinus latifolius*, *Hypochaeris radicata*, *Hieracium albiforum*, and *Xerophyllum tenax*), willow leaves (*Salix coulteri*), and bracken fern (*Pteridium aquilinum*; Mozejko 1971). Hares also readily consumed a non-native plant, spotted catsear (*Hypochaeris radicata*), in western Washington (Radwan and Campbell 1968).

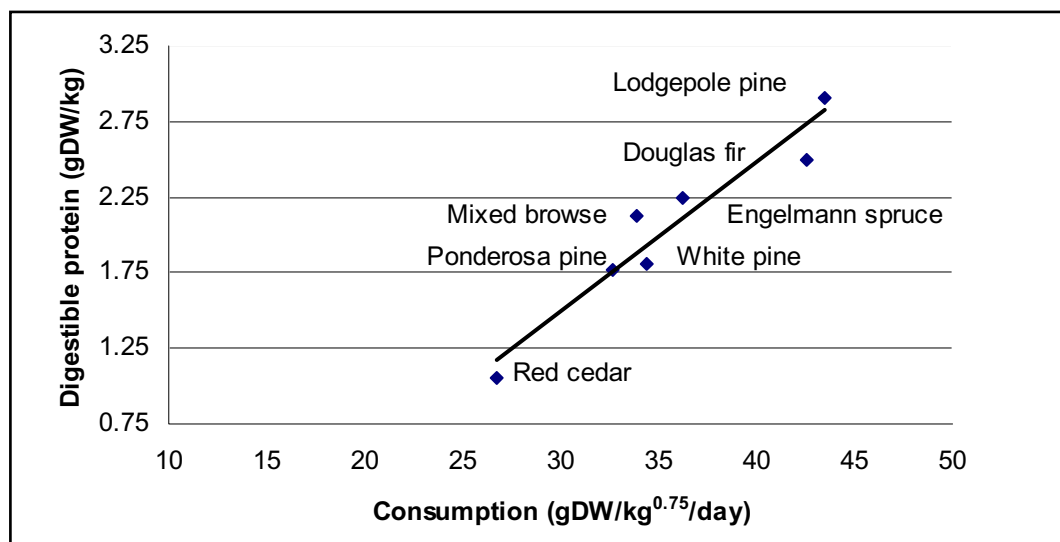


Figure 8. Captive snowshoe hare dry matter intake of Douglas-fir ($n = 4$), Engelmann spruce ($n = 6$), lodgepole pine ($n = 8$), ponderosa pine ($n = 3$), western red cedar ($n = 4$), and western white pine ($n = 4$), as well as a mixed browse ration ($n = 8$; comprised of 43% lodgepole pine, 21% Douglas-fir, 21% Engelmann spruce, and 11% white pine) in relation to digestible protein during single-species feeding trials in northern Idaho in 2000-01 and 2001-02 (revised from Ellsworth and Murray in prep. b).

Summer nutrition as a limiting factor on snowshoe hares has been largely discounted because of the diverse and superabundant supply of food available. Summer diet selection and nutrition were studied in the Yukon (Seccombe-Hett 1999), but we know of no nutritional analyses of summer foods conducted in the Rocky Mountains, much less a study examining the effects of summer nutrition on population ecology. However, we believe that such studies are warranted because the frequency and size of litters might be responsive to the direct and short-term effects of summer nutrition. While overbrowsing is not likely to be a factor during summer, nutritional stress may occur in lactating females which have increased energy demands (Whittaker and Thomas 1983). Moreover, the long-term impact of a poor diet early in the life of young mammals can be profound (Lindström 1999, Lummaa and Clutton-Brock 2002). White (1993) hypothesized that the nutrition of lactating female hares and the diet of young soon after being weaned could have important demographic consequences. In cyclic populations, changes in the abundance of snowshoe hares are linked to juvenile survival (Green and Evans 1940a, Meslow and Keith 1968, Keith and Windberg 1978), which White (1993) suggests might be correlated with their nutritional status during development. Seemingly small differences in forage condition during the spring and summer could predispose young hares to different survival probabilities and future reproductive output.

Demography

Reproduction

Murray (2003) summarized results from 27 studies and found that the number of young produced annually

per female varies from 5.6 to 13.4, with large variation in the number of litters per year (1.7 to 3.8) and average litter size (1.92 to 5.91). First litters are consistently smaller than later litters, but first-litter pregnancy rate tends to be high and declines with successive litters. In cyclic populations, much of the variation in litter size, pregnancy rates, and annual fecundity is associated with the cyclic phase (Keith and Windberg 1978, Cary and Keith 1979, O'Donoghue and Krebs 1992, Hodges et al. 2001, Stefan and Krebs 2001). Total annual natality is highest in the low phase, followed by increase, peak, and decline phases (Meslow and Keith 1968, Cary and Keith 1979). During the decline phase, the reproductive capability of adult females may be reduced because they lose more winter weight (Keith and Windberg 1978), are generally in poor condition (Keith et al. 1984), and are chronically stressed (Boonstra 1998a).

Relatively less is understood about patterns and variability of hare reproductive output in the Rocky Mountains because only a few studies have measured annual productivity, and these have been short-lived (**Table 2**). In general, Murray (2000) found that hares from western areas produce larger, but fewer litters, than those from eastern areas. Total annual productivity was lower in Rocky Mountain populations (range = 5.6 to 11.5 young per female; **Table 2**) compared to other hare populations (range = 7.6 to 13.4 young per female; reviewed in Murray 2003). Possible causes of low productivity include poor food resources (Vaughan and Keith 1981, Boutin 1984a, Murray et al. 1998), high stress levels caused by high predation risk (Boonstra and Singleton 1993, Boonstra et al. 1998a), shortened breeding season at higher elevations (Murray 2000), and reduced reproductive capabilities of adult females because hares in their southwestern range

Table 2. Annual reproductive output of snowshoe hare populations in the U.S. Rocky Mountains.

Study area	Study length (years)	Annual litters/female	Pregnancy rate (%) ^a	Female productivity (young/female)					Reference
				Litter 1	Litter 2	Litter 3	Litter 4	Annual	
Colorado	3	2.1	78	2.9	4.8	0.6	—	8.2	Dolbeer and Clark 1975
Utah	2	2.3	86	3.8	6.5	2.2	—	11.5	Dolbeer and Clark 1975
Idaho	2	3.2	64	1.7	1.8	1.2	1.0	5.7	Wirsing and Murray 2002
Idaho	3	2.8	95	1.8	1.7	2.7	—	6.2	Ellsworth unpub. data
Montana	2	—	—	2.8 ^b	3.7 ^b	1.8 ^b	—	8.3 ^b	Griffin 2004a
Montana	2	2.9	80	—	—	—	—	—	Adams 1959

^aCumulative rate for all litters.

^bCalculated from Table 4 in Griffin (2004)

generally have smaller body mass than northern hares (Nagorsen 1985). Of these, only food quality has been experimentally tested in the Rocky Mountain Region, but this was rejected as a cause of low productivity because food supplementation failed to improve reproductive parameters (Ellsworth and Murray in prep. b).

Mortality

Mortality rates of hares have been inferred from mark-recapture studies, and by directly measuring radio-collared hares. In a literature review of 19 mark-recapture studies, Murray (2003) found that adult hares tended to have higher annual rates of survival (average = 28 percent; range = 2 to 60 percent) than juveniles in the first year of life (average = 15 percent; range = 1 to 36 percent). However, mark-recapture studies overestimate mortality because they do not account for dispersed individuals (Boutin and Krebs 1986, Murray 2003). Radio-telemetry studies show that the survival rates of adults are higher than of juveniles in some cases (Keith 1990, Hodges et al. 2001, Wirsing et al. 2002a), but they are nearly equivalent in other populations (Keith et al. 1993, Gillis 1998). There is some evidence that smaller hares (i.e., juveniles) are disproportionately vulnerable to predation, perhaps because they were slower and less able to escape (Wirsing et al. 2002a, Wirsing 2003); however, the body condition of hares apparently has little influence on their vulnerability to predators (Murray 2002, Wirsing et al. 2002b).

Only a few studies have estimated survival of hares in the western United States. Leveret survival from birth to 53 days was estimated to be 67 percent based on mark-recapture events (Adams 1959) and 56 percent during the first 35 days of life based on radio-telemetry (Griffin 2004). Post-weaned hare survival in the western United States ranges from 9 to 59 percent (**Table 3**).

Seasonal patterns of survival were not consistent among studies; survival was highest during the winter in one study (E. Ellsworth unpublished data), but hare survival was highest in summer in others (Wirsing et al. 2002a, Abele 2004, Griffin 2004). In northern populations, more hares die during winter or early spring than during summer (Green and Evans 1940b, Keith and Windberg 1978, Keith et al. 1984, Boutin et al. 1986, Krebs et al. 1986). There is some evidence that hare survival in the Rocky Mountains is influenced by habitat conditions; survival was higher in dense stands than in open stands (**Table 4**; Griffin 2004), and in young forests that were unthinned, as opposed to those that were precommercially thinned (Bull et al. 2005). Conversely, no difference in survival rates was found between open and closed habitats in another study (Wirsing et al. 2002a), and precommercial thinning did not influence survival in western Oregon (Abele 2004).

Dispersal

There is large variation in dispersal rates among studies, ranging from 50 percent of juveniles (Gillis and Krebs 1999), 22 to 37 percent of all hares (Boutin et al. 1985, Keith et al. 1993, Wirsing et al. 2002a, Griffin 2004), to below 10 percent (Hodges 1998, E. Ellsworth unpublished data). The cues that trigger mammals to disperse are not always well understood, but some possible proximate mechanisms include intraspecific aggression, which can be elevated due to overcrowding, food supply, and vulnerability to predation (Dufty and Belthoff 2001). In northern populations, hares dispersed at higher rates during the early peak and early decline (Windberg and Keith 1976, Boutin et al. 1985), or during the increase phase (Keith and Windberg 1978, Wolff 1980), which indicates that hares may disperse as a result of overcrowding or low food supplies. Support for this notion comes from the finding that dispersers tend to be in worse body condition than non-dispersers

Table 3. Average annual survival rates (%) of juvenile (post-weaned hares in the first year of life) and snowshoe hares in the western United States.

Study area	Study length (years)	Estimation method	Juvenile survival (%)	Adult survival (%)	Cumulative survival (%)	Reference
Colorado	2	mark-recapture	25	45	—	Dolbeer and Clark 1975
Idaho	2	radio-telemetry	—	—	16	Wirsing et al. 2002a
Idaho	≈3	radio-telemetry	19	22	20	E. Ellsworth unpub. data
Montana	≈3	radio-telemetry	10-31 ^a	13-34 ^a	—	Griffin 2004a
Montana	2	mark-recapture	9	22	12.5	Adams 1959
Oregon	2	radio-telemetry	—	—	17-59	Bull et al. 2005
Oregon	2	radio-telemetry	—	—	17	Abele 2004

^aCalculated from Table 7 in Griffin (2004).

Table 4. Seasonal survival (adults and juveniles) and annual fecundity of female snowshoe hares. Fertility, the expected number of female leverets per female adult, was calculated as the sum of fertility rates in each birth pulse discounted by mothers' expected survival and the leverets' expected survival until the beginning of fall. Revised from Table 7 in Griffin (2004).

Habitat type	λ	Adult survival				Juvenile survival				Fertility
		Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	
Dense mature	1.14	0.706	0.854	0.711	0.804	0.683	0.841	0.688	0.787	2.15
Dense young	0.807	0.628	0.810	0.633	0.748	0.604	0.795	0.610	0.730	2.10
Open mature	0.413	0.508	0.734	0.515	0.652	0.476	0.712	0.483	0.626	1.99
Open young	0.413	0.508	0.734	0.515	0.652	0.476	0.712	0.483	0.626	1.99

(Windberg and Keith 1976, Boutin et al. 1985), and juveniles in overcrowded habitats are more likely to move (Keith and Surrndi 1971). Possibly, emigrants tend to be substandard individuals that vacate their home range to avoid competition for mates and food resources. However, food supplementation did not prevent extensive dispersal in some populations (Boutin 1984b, Gillis and Krebs 1999, Murray 1999), and dispersal still occurred when densities were low and food supplies appeared adequate (Wirsing et al. 2002a, Ellsworth and Murray in prep. a). Another possible proximate cause of dispersal is that hares might vacate areas where they are more vulnerable to predators. Hares disperse at higher rates from small habitat patches where exposure to predators might be higher (Keith et al. 1993); dispersal rates were higher in low than high cover sites (Wirsing et al. 2002a), and dispersing hares tended to settle in dense versus open sites (Griffin 2004).

Geometric rate of natural increase

Demographic modeling enables predictions to be made about whether a population will increase, decline,

or remain stable. Population projection models and similar analyses allow ecologists to make quantitative predictions about how populations will change, which can help elucidate selective and demographic pressures on an animal population and enable recommendations for species management.

A study in Montana evaluated the growth rate (λ) of snowshoe hare populations based on juvenile and adult survival, and fertility rates (Griffin 2004). Corresponding to their model, we present a graphical representation in the form of a life cycle graph (Caswell 2001), which is an alternative way of depicting the projection methods that are used to evaluate the current status of a population (**Figure 9**). The purpose of Griffin's study was to examine variation in hare demography across a heterogeneous landscape, and to explore whether some habitat types functioned as sources or sinks. Large differences in λ existed among habitat types (**Table 4**). Dense forest types appeared to be sources while open forests acted as sinks. Although sensitivity or elasticity analyses were not performed, Griffin (2004) suggests that annual survival in these forest stands likely has a

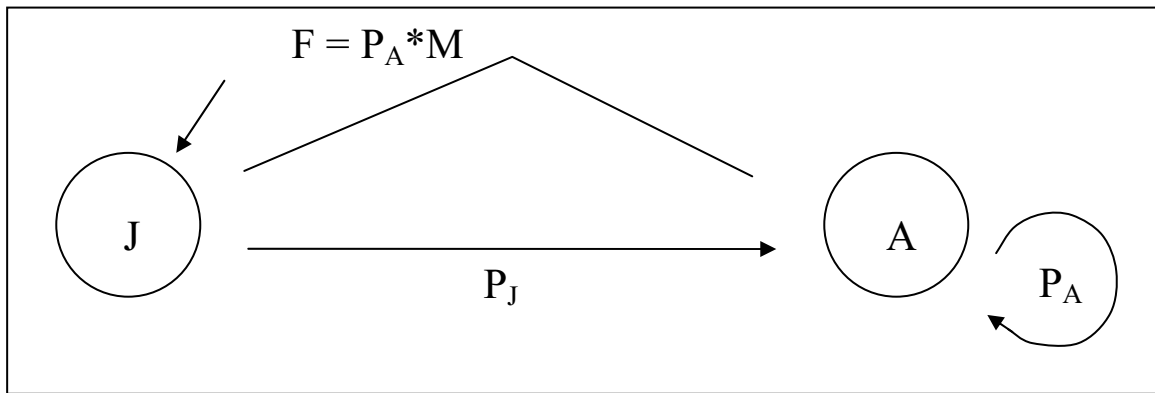


Figure 9. Two-stage life cycle graph for snowshoe hare. The lettered circles (nodes) represent juvenile (J) and adult (A) stages of the life cycle graph. The arrows (arcs) connecting the nodes represent vital rates or transitions between stages (i.e., survival (P), fertility (F)). M represents the number of female offspring produced per female. For a complete description of the use and construction of life cycle graphs refer to Caswell (2001).

greater impact on λ than fertility, despite generally low reproductive rates. Because hares had higher survival in dense than open stands, this finding emphasizes the importance of vegetation structure for hares in the Rocky Mountains, and suggests that landscape heterogeneity disrupts population continuity and perhaps contributes to the apparent lack of pronounced population cycles (Griffin 2004).

Elasticity and sensitivity analyses are also valuable demographic modeling tools. Elasticity analysis allows ecologists to estimate and compare the effects of changes in survival, growth, or reproduction of particular life stages, as well as the proportional contribution of different aspects of the life cycle to population growth rate (Caswell 2001). Sensitivity analysis measures the change in λ resulting from a change in a focal parameter. In the Yukon, demographic parameters from a cyclic snowshoe hare population were incorporated into a population projection model, and estimates were compared to known annual population change and elasticities and sensitivities were calculated (Haydon et al. 1999). Results show that during the low-increase- and high-phase λ was most sensitive to juvenile survival, followed by adult survival, than by fertility (**Table 5**). However, adult survivorship appears to be a more important determinant of the rate of population change during the decline-phase. Consistent with these findings, juvenile survival was the most sensitive demographic parameter throughout the population cycle in Alberta (data from Keith and Windberg 1978, see Haydon et al. 1999), and it was believed to be an important and sensitive demographic parameter in other populations (Green and Evans 1940a, Meslow and Keith 1968, Keith 1981, Krebs et al. 1986). In Colorado, it was estimated that juvenile annual survival rate needed to be about 16 percent for the population to remain in balance (Dolbeer and Clark 1975). Including adults and juveniles, an annual survival rate exceeding

28 percent appears to be required for hare population growth in the Yukon (Hodges et al. 2001).

Community ecology

Snowshoe hares are an important component of Rocky Mountain forest communities, especially within the subalpine zone. Although their ecological role in these communities is understudied, hares are major prey items for a variety of predators, consume large amounts of woody browse, and deposit large amounts of fecal material across the forest floor. However, it is unlikely that hares play as pivotal a role here as they do in boreal forests. In Canada and Alaska, much of the forest community hinges on hare abundance. Plant growth and chemistry, the demographics and behavior of predators (e.g., lynx, coyotes, and great-horned owls), and the dynamics of other prey populations are all intimately tied to hare population cycles (Sinclair et al. 2001, Ruesinik et al. 2002). If hare populations are reduced or experience a disruption of the cycle, it is believed that profound changes would occur throughout boreal ecosystems (Sinclair et al. 2001). Such a dramatic impact in Rocky Mountain communities is less likely because of the diversity and spatial complexity found within the Rocky Mountains, and hares are not as abundant and widespread in their distribution as they are in boreal forests. Hence, it is questionable whether predators rely extensively on hares to persist in the Rocky Mountains, and it is not believed that hares here have had a strong evolutionary influence on plant growth patterns or production of chemical defenses against herbivory (Swihart et al. 1994, Wirsing and Murray 2002). Current understanding of hares within these forests, then, suggests that hares have a less widespread community impact, with more significant roles being relegated to only a few habitat types at mid to high elevations, i.e., lodgepole pine and spruce-fir forests. Of course, this conclusion is tentative, and we emphasize

Table 5. Sensitivities and elasticities for the principal snowshoe hare demographic parameters of a population in the Yukon. Revised from Haydon et al. (1999).

Parameter	Sensitivity	Elasticity
28-day juvenile postweaning survival	19.03	7.14
28-day adult survival	13.08	4.95
30-day Prewaning survival	3.45	0.85
1 st litter	0.11	0.15
2 nd litter	0.11	0.30
3 rd litter	0.11	0.25
4 th litter	0.09	0.15
4 th litter pregnancy rate	0.44	0.15

that focused research is required to develop a better and more specific understanding of how hares interact with other species in Rocky Mountain communities.

In the following sections, we discuss interactions between snowshoe hares, their predators, and competitors in the Rocky Mountains. We also developed

a web of ecological relationships for snowshoe hares (**Figure 10**), following Andrewartha and Birch (1984). This envirogram is a representation of the proximal (centrum) and distal factors (web) thought to affect snowshoe hare distribution and abundance. The relative importance of these factors is not represented.

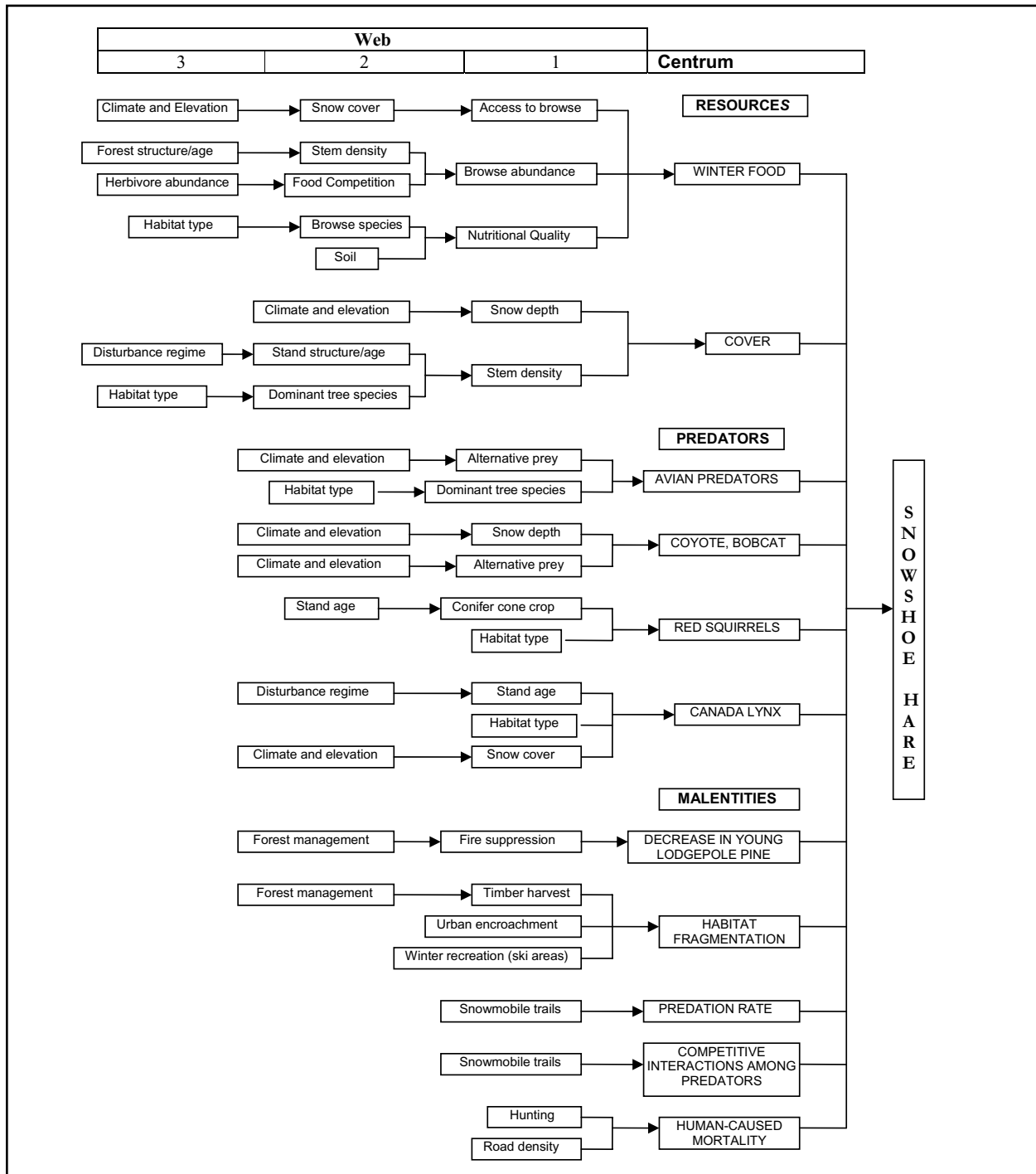


Figure 10. Envirogram representing the web of linkages between snowshoe hares and their environment in the Rocky Mountains (Andrewartha and Birch 1984).

Effects of hare herbivory on the potency of plant defense chemicals: biogeographic variability as an indicator of browsing intensity

The value and palatability of a plant to an herbivore are largely characterized by nutritional content as well as the assortment of chemical defenses that a plant contains. Woody plants are particularly rife with toxic or digestion-inhibiting compounds, but potencies vary substantially among species, by plant age, and with growing environment (Robbins 1993). The evolutionary history of plant-browser interactions is also believed to play an important role in the specificity and strength of defenses. It is hypothesized that in areas where browsing pressure is historically intense, plants are selected to produce stronger and more specific chemical defenses than in areas where browsing is lower (Dethier 1954, Ehrlich and Raven 1964, Berenbaum 1983, Cornell and Hawkins 2003). Based on this reasoning, it was proposed that the primary forage species in high-density hare populations (i.e., boreal forests) should produce stronger and more specific chemical defenses than plants in lower density populations, including the Rocky Mountains (Bryant et al. 1989, 1994, Swihart et al. 1994, Swihart and Bryant 2001). It follows that diet selection should reflect biogeographical gradients in the effectiveness of plant chemical defenses, such that consumption is less affected by chemical defenses in low-density than high-density populations. Two feeding studies support this: 1) plants with high concentrations of defense compounds were generally avoided by hares in boreal forests (Rodgers and Sinclair 1997), and 2) consumption was largely unaffected by conifer defense concentrations (total monoterpenes and phenols) in the Rocky Mountains (Wirsing and Murray 2002). In this second study, consumption rates were correlated instead with plant protein, and it was argued that hares were simply able to select the most nutritious plants because chemical defenses were weak (Wirsing and Murray 2002). These conclusions remain tentative, however, because specific chemical defenses have yet to be evaluated and some variability in the efficacy of protein-inhibiting compounds was apparent among Rocky Mountain conifers (Ellsworth and Murray in prep. a). Furthermore, herbivory can induce browse species to produce chemical defenses, and the degree to which Rocky Mountain plants are induced by hare herbivory is unknown. In contrast, extensive research has been conducted in boreal forests showing that a range of woody plant species produce strong chemical defenses when they are browsed by hares (Bryant 1981, Reichardt et al. 1984, Bryant et al. 1985, Sinclair et al. 1988b, Jogia et al. 1989, Reichardt et al. 1990a, b, Bryant et al. 1991).

Hares and their predators: Interactions in the Rocky Mountains

Native mammalian carnivores in the Rocky Mountains of the United States that are known to kill post-weaned hares include gray wolf, coyote, red fox, mountain lion, bobcat, lynx, wolverine, fisher, and American marten. Avian species include northern goshawk, red-tailed hawk, golden eagle, great-grey owl, great-horned owl, barred owl, and common raven (see Causes of death section). However, the guild of predators that hunt hares can be seasonally and spatially variable in the Rocky Mountains. This is highlighted by a comparison of proportions of hares that were taken by predator classes in two Idaho studies: canids, 44 and 29 percent; raptors, 21 and 21 percent; felids 0 and 16 percent; and mustelids, 13 and 1 percent; 21 and 26 percent could not be classified according to predator type (Wirsing et al. 2002b, E. Ellsworth unpublished data, respectively).

Snow conditions (i.e., depth and density) probably play an important role in the types of predators that hunt hares during the winter, and thus may influence predation risk. For predatory mammals, snow conditions can significantly influence energy expenditure, hunting success, movement patterns, and distribution. Movements of mammals with a high foot-loading, such as coyote or bobcat, are impaired by deep snow conditions more than animals with lower foot-loading, such as Canada lynx (Todd et al. 1981, McCord and Cardoza 1982, Koehler and Hornocker 1989, Murray and Boutin 1991, Murray et al. 1994, Crete and Lariviere 2003, Kolbe 2005). Canada lynx are adapted to movement in deep snow and, consequently, are able to consistently kill hares in these conditions (Murray et al. 1994, Stenseth et al. 2004). Where lynx are absent, hunting pressure on hares may be significantly reduced during the winter. In northern Idaho, bobcat and coyotes were major predators from spring through fall, but these predators largely vacated the study area from mid-December through early March, at a time when unconsolidated snow typically exceeded 1 m (E. Ellsworth unpublished data). Correspondingly, the proportion of radio-collared hares that succumbed to predators was lower during the winter than in other seasons (**Figure 11**). In areas where predators remain year-round, it is unknown whether generalist predators specialize on hares as they do in boreal forests (e.g., great-horned owls and coyote; O'Donoghue et al. 2001), but Adams (1959) estimated that hares comprised nearly half the diet of great horned owls in Montana.

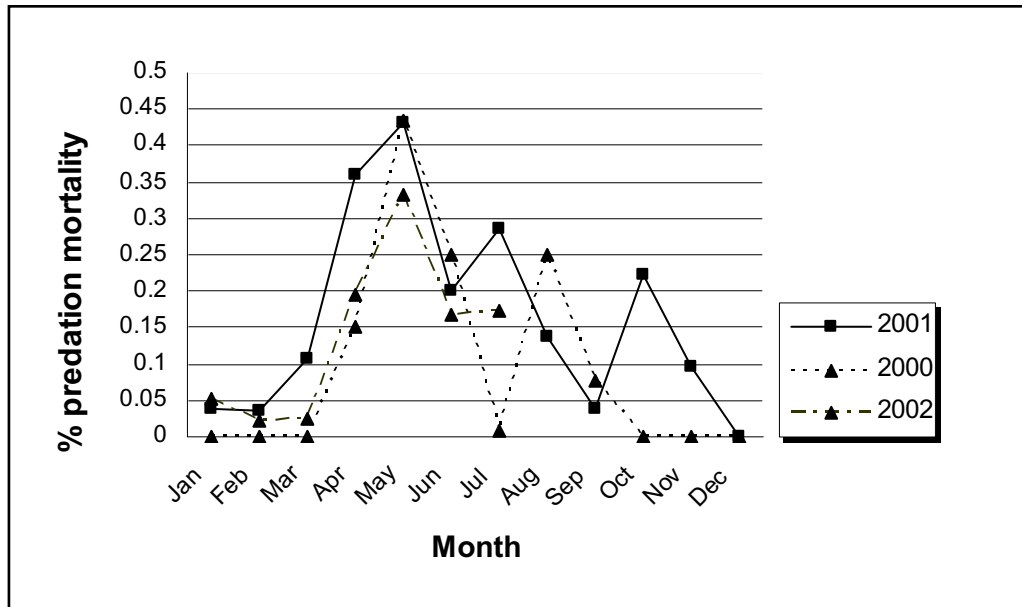


Figure 11. Percent of radio-collared snowshoe hares that were killed by predators each month during 2000, 2001, and between January and July in 2002 on the Idaho Panhandle National Forest (E. Ellsworth unpublished data). The number of radio-collared hares in 2000 ($n = 119$), 2001 ($n = 128$), and 2002 ($n = 65$), varied monthly (range: 23 – 73).

Canada lynx and snowshoe hares in the Rocky Mountains

Canada lynx populations have declined throughout much of the southern portions of their range and were listed in 2000 as threatened in the contiguous United States under the Endangered Species Act (U.S. Fish and Wildlife Service 2000). Lynx conservation has therefore become of critical interest. Two documents synthesize lynx population history and identify important elements to lynx ecology (Ruediger et al. 2000, Ruggiero et al. 2000). Within Region 2, only Colorado has a finalized lynx conservation plan (CDOW 2002). However, lynx have not been well studied in the western United States, and there are gaps in our understanding of lynx ecology that need to be filled to develop a strong conservation plan.

Core lynx populations in the Rocky Mountains:

Lynx are specialist predators of snowshoe hares, and their abundance across North America closely mirrors the distribution of forest types where hares are a dominant component of ecological communities. Lynx are comparatively abundant and widespread at the heart of their geographic range in Canada and Alaska boreal forests where hares are ubiquitous and reach high densities during the cyclic high phase (Parker et al. 1983, Poole 1994, O'Donoghue et al. 1995, Mowat et al. 1996, O'Donoghue et al. 1997, Poole 2003). They are far less common along the southern periphery of their

range in the United States and southern Canada, where hare populations are lower and patchily distributed, but more stable.

In the U.S. Rocky Mountains, lynx have been historically documented in many areas (McKelvey et al. 2000a), but breeding populations persist in only a few (**Figure 12**; Koehler and Aubry 1994, Ruediger et al. 2000). Habitat selected by lynx in the Rocky Mountains appears to correspond to the type of habitat where the highest hare densities occur. Core lynx areas are characterized by rolling, deeply-forested mountains at mid- to high elevations that receive substantial snowfall (McKelvey et al. 2000a). Conversely, lynx tend to avoid open terrain and steep and dry mountains where hare density is typically low. Among core areas, however, there are differences in habitat associations, and it is useful to partition extant Rocky Mountain lynx populations into three geographical sub-groups: northern (along the Canadian border in Washington, Idaho and Montana), central (the Greater Yellowstone Ecosystem [GYE] and other ranges in northwestern Wyoming), and southern (Rocky Mountains of Colorado and southern Wyoming) (**Figure 12**). One notable habitat difference is that in the northern and GYE regions, young lodgepole pine forests appear to be more important to lynx (and hares) while in Colorado, spruce-fir habitat appears to be more important. As a case in point, lodgepole pine does not occur naturally in the San Juan Mountains of southern Colorado where

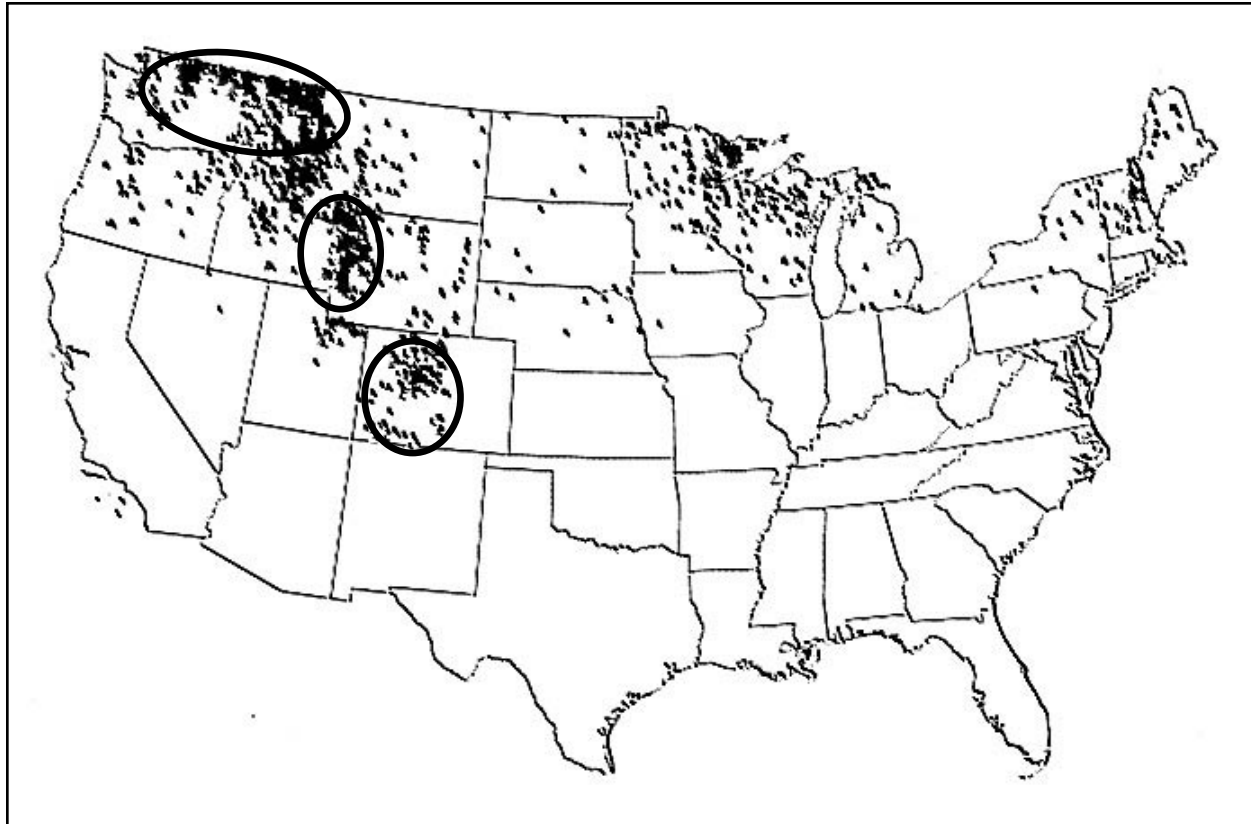


Figure 12. Lynx occurrence data in the United States (excluding Alaska) from 1842-1998. Core breeding areas in the western United States are circled. Revised from McKelvey et al. (2000a). Reprinted with permission, University Press of Colorado.

lynx have been reintroduced (Colorado Gap Analysis Project Report [<http://ndis1.nrel.colostate.edu/cogap/cogaphome.html>]). It also makes sense to treat these three core areas separately because they are separated by a substantial distance and are not well connected by forested corridors, particularly between the southern and central Rocky Mountains (Findley and Anderson 1956), which are separated by large gaps in suitable habitat. Although lynx are wide-ranging and can disperse long distances across unsuitable terrain (Mech 1980, Slough and Mowat 1996, Poole 1997), there is little evidence of movement among these three zones.

Historically, the most robust lynx populations in the U.S. Rocky Mountains have been near the Canada border from western Montana to the Okanogan Plateau in northern-central Washington. Trapping records, museum specimens, observations, and more recent population and ecology studies document that lynx have persisted within a few discrete pockets of habitat across this belt of forested mountains (McKelvey et al. 2000a, Ruediger et al. 2000). The genetic structure of Montana lynx populations indicates occasional influxes of animals from Canada (Schwartz et al. 2002, 2003). Lynx in the

western United States use a variety of forest types, but they are most strongly associated with young to middle-aged lodgepole pine forests that house relatively dense hare populations (Koehler 1979, Koehler 1990a, b, McKelvey et al. 2000a, b, von Kienast 2003). There is concern, however, that lynx have declined since historical times (McKelvey et al. 2000a), perhaps partly because fire suppression over the past 150 years has reduced the extent of young lodgepole pine forests (Aubry and Koehler 1994). As we discuss below, hare density even within prime hare habitat in the Rocky Mountains may be marginal for lynx, and reductions in early successional lodgepole pine cover types could have substantial negative implications for lynx. In fact, there are areas in the panhandle of northern Idaho and northeastern Washington where lynx were regularly observed and trapped for several decades following extensive fires in the early 20th century. As these forests have matured, however, lynx have again become rare (E. Ellsworth personal observation, T. Layser personal communication 2001). Similar scenarios involving forest maturation have probably occurred in areas along the north-central Idaho and Montana border, in portions of north-central Washington (Washington

Department of Wildlife 1993), and in northern Montana (Koehler 1990a).

Lynx in the GYE and nearby mountain ranges in western Wyoming and southeastern Montana have been poorly studied, and little information is available regarding the interaction between hares, habitat, and lynx. The paucity of lynx data is partly due to low human density and large tracts of wilderness that exist in this region. However, historic and recent records document only a few cases of breeding lynx, and the low number of lynx observations suggests that lynx populations are small (Reeve et al. 1986, McKelvey et al. 2000a, Squires and Laurion 2000, Squires et al. 2003, Murphy et al. 2004). One possible explanation for temporal and spatial fluctuations in lynx abundance is that lynx may track regional population changes in hare density, which are in turn closely tied to the successional stage of mid-elevation lodgepole pine forests. Given the extensive distribution of lodgepole in the GYE, we believe that the GYE has the potential to support substantial lynx populations during times when young to middle-aged lodgepole forests dominate the landscape, but it is substantially less suitable when forests mature. The validity and strength of this argument should be addressed over the next half-century because the extensive 1988 fires provide a natural experimental template (Murphy et al. 2004). Based on the large extent of regenerating lodgepole pine forests in the GYE, we expect lynx populations to grow over the next several decades. However, this prediction is tempered by the realization that the condition of forests before the 1988 fire, fire intensity, and local landscape features influence the structure and capability of young lodgepole pine forests to regenerate and provide high-quality hare habitat (Anderson et al. 2004). Hares might not be uniformly dense across the post-fire landscape, and ongoing studies show substantial variability in hare density in these young forests (K. Hodges personal communication 2005, L.S. Mills personal communication 2005).

In Colorado and southern Wyoming, a relatively insular population of reintroduced Canada lynx exists at the southernmost extent of their geographic range (Shenk 2001, 2005). This lynx population is comprised of approximately 140 adult lynx from Canada that were released between 1999 and 2005, and it appears to be thriving as evidenced by a high number of surviving kittens produced from 2003-2005 (>40 offspring; Colorado Division of Wildlife; dowinsider.wildlife@state.co.us). Prior to reintroduction efforts, Colorado was occupied by declining numbers of lynx throughout much of the 20th century; they may have been extirpated

during the 1990's (McKelvey et al. 2000a), but the status of native lynx remains highly uncertain. The decline of Canada lynx in Colorado was likely precipitated by widespread trapping, intensive predator control, and loss of forests to cutting and fires in the ore belts as the mining industry boomed (Aubry et al. 2000b, Ruediger et al. 2000). Without historic snowshoe hare population data, it is impossible to assess whether hare population abundance played a role in lynx abundance, but it is possible that habitat changes associated with the mining boom in the 1800's could have negatively influenced hares, and thus impacted lynx. Given the success of lynx recovery efforts over the past seven years, current forest conditions and hare density are apparently suitable for lynx persistence in at least parts of the southern Rocky Mountains (Colorado Division of Wildlife; downside.r.wildlife@state.co.us). However, lack of widespread regeneration of lodgepole pine forests may negatively influence hare density and, therefore, lynx populations in other parts of the system.

Lynx persistence: hare abundance and distribution requirements in the Rocky Mountains: In southern habitats, two important and interrelated questions have arisen regarding the lynx/hare relationship: 1) how dense do hare populations need to be to sustain lynx? and 2) what sort of landscape arrangement of prime hare habitat is necessary for lynx? The first question was addressed by Ruggiero et al. (2000), who qualitatively estimated that given minimum prey requirements, over 0.5 hares per ha were required for persistence (Mowat et al. 2000), and by Steury and Murray (2004), who found that lynx in northern forests required a minimum density of 1.1 to 1.8 hares per ha, based on models of how lynx populations in northern forests respond demographically to changes in hare density (Steury and Murray 2004). In cyclic hare populations, this threshold is consistently surpassed during increase, peak, and decline phases, and hare density only drops below this during cyclic lows (Hodges 2000a). In the Rocky Mountains (and other southern areas), this apparent minimum requirement is only marginally met, and hare density is often below the threshold even in habitats considered to be favorable (i.e., young dense conifer forests; **Table 1**). Also, hare density estimates derived from mark-recapture studies could overestimate abundance at a landscape level because researchers often target their efforts within pockets of prime hare habitat and avoid low-quality habitat.

How then, do lynx persist in some areas, and how is it that lynx appear to be faring well after their reintroduction into Colorado? One answer is that lynx

might require fewer hares in the Rocky Mountains than elsewhere. The model developed by Steury and Murray (2004) included parameters only from boreal forests, and lynx requirements have not been explicitly examined in the Rocky Mountains. It is possible that southern lynx need fewer hares per area because they might 1) take advantage of the broader prey base available in southern environments (G. Patton personal communication 2006), 2) expend less energy, and/or 3) have higher hunting success. There is little indication that lynx consume fewer hares in the Rocky Mountains than elsewhere (Koehler and Aubry 1994, Squires and Laurion 2000), but food studies in the western states are limited and no studies have yet to be published on reintroduced lynx in Colorado. This is an important shortcoming because lynx probably have a broader available prey base in lower latitude forests than in northern forests. In boreal forests, major lynx prey is limited to hares, red squirrels, grouse, and occasionally song birds. In contrast, lynx habitat in Colorado contains a greater bird and small mammal diversity, and two additional leporids (white-tailed jackrabbit [*Lepus townsendii*], mountain cottontail [*Sylvilagus nuttallii*]). Moreover, red squirrels, which are the most important alternate prey for lynx, are often abundant in spruce-fir forests (Obbard 1987).

Lynx also may require less food to fuel expenditures because energy costs may be reduced in the more moderate climates of the Rocky Mountains. Finally, lynx might be more proficient hare hunters in the Rocky Mountains. Two features of these southern mountains suggest that this could be the case. First, the snow surface is usually firm for longer periods during the winter in the Rocky Mountains than it is in boreal forests (Stenseth et al. 2004). This benefits lynx because hunting success rates tend to increase when the snow surface is firmer (O'Donoghue et al. 1998, Stenseth et al. 2004). Second, lynx may have higher hunting success in spatially heterogeneous environments. Prey can be more vulnerable in patchy rather than continuous habitat, partly because of the negative effects of increased and concentrated predatory effort (Schneider 2001).

A second broad question concerning hares and lynx involves the area and spatial configuration of hare habitat that is necessary to sustain lynx in the Rocky Mountains. Buskirk et al. (2000) suggest that most suitable habitat patches in the Rocky Mountains are not large enough to encompass a lynx home range, and therefore home ranges must necessarily be larger in order to support a lynx. In fact, lynx have a larger average home range size in southern forests (151 km²)

than in northern forests during the cyclic high- (62 km²) or low-phase (103 km²; Aubry et al. 2000b); this is consistent with the negative relationship between lynx home range size and hare density (Mowat et al. 2000, Poole 2003). However, there is undoubtedly a ceiling on lynx home range size, as well as limits to the ruggedness of terrain through which lynx will travel on a regular basis to access suitable habitat.

Competition for food with other species

Because hares consume many of the same plant species as moose (*Alces alces*), white-tailed deer (*Oedocoileus virginianus*), and mule deer (*O. hemionus*), there is potential for food competition (Hough 1949, Dodds 1960, Bookhout 1965b, c, Telfer 1972, Wolff 1980). However, competition is reduced because ungulates and hares tend to forage at different heights (Dodds 1960, Bookhout 1965b, c, Oldemeyer 1983), summer food is superabundant, and most ungulates vacate areas with deep snow. Thus, food competition probably only occurs when snow cover is low. Furthermore, competition is more likely to occur between hares and moose than hares and deer because moose can tolerate deeper snow than deer. The possibility of moose-hare competition is limited as well, however, because moose in the Rocky Mountains tend not to browse conifers heavily during the winter (J. Dungan personal communication 2005). Although no specific research has been done on dietary overlap between hares and ungulates in the Rocky Mountains, this topic is perhaps an area of interest because moose have been introduced into three areas of Colorado (Grand Mesa, North Park, and Creede), and their range is expanding (Fitzgerald et al. 1994).

CONSERVATION OF SNOWSHOE HARE IN REGION 2

Threats

Snowshoe hare populations are susceptible to changes in the distribution and character of subalpine forests in Region 2. Hares are near the southern boundary of their geographical range here, and although they are common in some areas, they are largely confined to a belt of mid- to high-elevation subalpine forests. Within this zone, hare abundance is not uniform, and the best habitat for hares (purported to be mature spruce-fir or young lodgepole pine) tends to be patchily distributed (Appendix A for distribution of spruce-fir and lodgepole pine forests in Colorado). Declines in the abundance of these forest types could change hare survival and dispersal patterns, decrease connectivity, isolate

some sub-populations, and reduce the capacity of the landscape to be a source for hare colonization of forests after disturbance. In general, the primary landscape-wide threats that could bring about such changes are climate change and forest management practices (e.g., fire suppression, silvicultural treatment including timber harvest). Other potential but less widespread threats include recreation development, mining, oil and gas exploration and development, snowmobile trails, and hunting.

Climate change

Anthropomorphic greenhouse gas emissions are predicted to raise global temperatures 1.5 to 4.0 °C (Houghton 2004). Predicted impacts of warming vary among forest types and depend on the magnitude of regional temperature increase, precipitation patterns, and sensitivity of plants, animals, and biological communities to these changes (Nielson et al. 1989, 2005).

In the southern and central Rocky Mountains, it is well established that there are strong links between climate and vegetation patterns. Over the last 18,000 years since the last glacial maximum, conditions have ranged from much colder to somewhat warmer than today, and plant species have reacted to these climate changes by advancing or shrinking their geographic and elevational distribution. On the Colorado Plateau, for example, dominant forest types have varied throughout the Holocene from primarily mixed-conifer, to pure Engelmann spruce, to ponderosa pine (Fall 1985, Anderson et al. 1999). The vegetation history of the Yellowstone region is also a series of plant expansions, invasions, contractions, and extinctions in response to climate change (Baker 1986, Whitlock 1993, Whitlock and Millspaugh 2001), and it is likely that future vegetation communities in the Rocky Mountains also will track climate fluctuations (Bartlein et al. 1997).

Winter and spring temperatures have risen during the 20th century in western North America, including Colorado and Wyoming (e.g., Folland et al. 2001, Mote et al. 2005), and most climate models project that average temperatures will continue to increase over the next few decades (Watson et al. 1998, Cubasch et al. 2001). Climate change could have mostly adverse effects on snowshoe hares, particularly if warmer temperatures lead to widespread declines in mid- to high-elevation spruce-fir forests. A warmer climate could, however, have a positive impact on hares in some instances if fire frequency increases and forests are converted to young lodgepole pine. In one scenario,

warmer temperatures in subalpine forests increase drought stress, fire frequency, and tree mortality due to insects and disease (Dale et al. 2001). As a result, the subalpine forest zone would be constricted, especially at lower elevations, by upward range expansion of drought tolerant species (e.g., ponderosa pine and Douglas-fir) into spruce-fir dominated forests (Romme and Turner 1991). Some subalpine forests also could be eliminated or increasingly isolated in drier and more southerly mountain ranges.

However, a key element in promoting forest change is moisture availability (Dale et al. 2001), and at this stage it is not clear whether moisture levels in the southern Rocky Mountains will decline concurrent with increasing temperatures. Although the depth and/or duration of the winter snowpack may be reduced in portions of the Rocky Mountains, annual precipitation in Colorado and Wyoming increased between 1950 and 1997 (Mote et al. 2005). It is possible that the deleterious effects on mid- to high-elevation forests that could arise from a warmer climate could be alleviated by increased moisture.

Silviculture

Commercial timber harvest can impact snowshoe hares at different temporal and spatial scales. Within a harvested stand, conditions for hares often follow a general pattern: 1) initially, understory cover is low and hares are absent, 2) after a few years woody shrubs and small trees regenerate and hares begin to reoccupy stands, 3) hare density peaks when trees are large enough to provide cover and food even during deep snowy winters, and 4) forests mature and hare populations decline as the understory decreases (Gashwiler 1970, Telfer 1974, Brocke 1975, Conroy et al. 1979, Wolfe et al. 1982, Litvaitis et al. 1985a, Monthey 1986, Sullivan and Moses 1986, Scott and Yahner 1989, Ferron et al. 1994, Darveau et al. 1998, Ferron et al. 1998, Potvin et al. 1999, Bellefeuille et al. 2001, Forsey and Baggs 2001, Abele 2004, Griffin 2004, Newbury and Simon 2005, Potvin et al. 2005a). In forest types where hare recovery follows this pattern, such as most lodgepole pine forests, logging can benefit hares for periods of time because mature forests are converted to early successional stages that hares favor for cover and forage (Sullivan and Moses 1986, Rogowitz 1988, Koehler 1990a, b). However, beneficial aspects of harvest are tempered by the fact that many hares vacate logged areas initially (Ferron et al. 1998, Potvin et al. 1999, Abele 2004), and some stands do not recover suitably, with recovery taking a long time in some environments. In certain forest types (most notably spruce-fir) or

locations, hares may prefer mature rather than young stands. Hares may not use some regenerating forests until the shrub and sapling understory exceeds 2 to 3 m (Potvin et al. 1999), and some forests never re-establish a sufficient understory for hares post-harvest (i.e., with an optimal stem density of <5,000 stems per ha; see Koehler 1990b).

In the Rocky Mountains, stand regeneration varies widely and is influenced by interactions between environmental variables including climate, topography, elevation, aspect, slope, soil moisture, and tree species composition. Therefore, forest managers should be cognizant of specific regeneration scenarios in different environments and among different forest types (Long 1995). In Colorado and Wyoming, harvest of lodgepole pine is probably mostly beneficial to hares if stands regenerate sufficiently. Conversely, hares may be negatively influenced by timber harvest in many spruce-fir forests. Hares are common in mature spruce-fir forests (Wolfe et al. 1982, Zahratka 2004, Miller 2005), but they tend to avoid very young spruce-fir forests, particularly during the winter, because these stands provide little food or cover until tree crowns extend at least a few meters above the snow surface (Wolfe et al. 1982). Hares probably do not fully reoccupy clearcut spruce-fir forests for several decades because regeneration following disturbance is a slow process even under the best of conditions. At these higher elevations, cold temperatures, high wind speeds, and deep snowfall combine to reduce biological activity, and the short growing season limits growth such that young Engelmann spruce and subalpine fir typically do not reach breast-height for 20 years or more (Fiedler et al. 1985, Long 1995). Although stand regeneration may be faster at some lower elevation sites where faster-growing lodgepole pine can be a dominant part of the early successional forest (Long 1995), large clearcuts remain essentially non-habitat for hares for lengthy periods, potentially compromising habitat connectivity and influencing hare movements.

Insufficient understory density is a particular problem in forests that are pre-commercially thinned (Sullivan and Sullivan 1988, Shaw 2002, Abele 2004, Griffin 2004, Ausband and Baty 2005, Bull et al. 2005), and in 1999 the USFS halted pre-commercial thinning on lands defined as lynx habitat. Live stems of young regenerating conifer forests in the western United States are commonly thinned from 3,000 to 6,000 stems per ha to 650 to 1300 stems per ha to accelerate tree growth, select for species of high value, and maximize timber yield (Johnstone 1995, Smith et al. 1997). Abele (2004) found that hares vacated thinned stands soon after timber

harvest; Sullivan and Sullivan (1988) and Griffin (2004) reported that hare densities declined in thinned stands for a few years post-cut. In contrast, Bull et al. (2005) found hare densities to be higher in unthinned than thinned stands. Although long-term impacts of thinning have not been sufficiently evaluated, there is some indication that there could also be beneficial aspects to thinning under some circumstances. Griffin and Mills (2004) employed a modeling approach to examine temporal effects of stand age, thinning regime, and patterns of succession on hare demographics. Results suggested that low levels of pre-commercial thinning may support as many hares as landscapes without thinning. Consistent with this model, a field study found that hare densities were highest in 50 to 60 year old lodgepole pine stands that had been thinned (Zimmer 2004). Zimmer (2004) suggests that hares might prefer these stands because thinning delayed the self-pruning process, and thus lower branches were available for a longer period of time than in unthinned stands.

Landscape level impacts of timber harvest on snowshoe hare are not well understood, but because hare habitat in the Rocky Mountains is naturally patchy, hare populations may be sensitive to further fragmentation. Hare survival is reduced in patchy environments (Wolff 1980 a, b, Wirsing et al. 2002a), and landscape conditions can affect the ability of hares to reoccupy regenerating clearcuts (de Bellefeuille et al. 2001). Indeed, hares seldom venture into large clearcuts more than 200 to 440 m from canopy cover (Brocke 1975, Conroy et al. 1979), and the size and density of clearcuts could be an important component for maintaining hare populations. Logging roads can indirectly affect hares as they impact landscape structure by decreasing mean patch size and by increasing edge density (McGarigal et al. 2001). Although logging roads are not barriers to hare movement or likely to reduce population connectivity, roads can facilitate travel of coyote and other predatory mammals (Dickson et al. 2005, Kolbe 2005), possibly influencing predation patterns.

Wildfire suppression

Fire disturbance is an important factor shaping Rocky Mountain subalpine forests (Veblen 2000), and it is recognized that maintaining disturbance regimes within a historic range of variability can sustain ecosystem structure and function (Morgan et al. 1994). For snowshoe hares, historic fire suppression in some Rocky Mountain forests may have reduced habitat quality, and we believe that efforts should be made to restore natural fire patterns especially within mid-elevation forests.

Wildfire in the Rocky Mountains can create high-quality habitat for snowshoe hares, particularly when fire is followed by the growth of dense stands of lodgepole pine, the archetypical post-fire tree species. However, there is some evidence that fire occurrence has declined in Rocky Mountain forests since the early 1900's, probably as a result of fire suppression (Grissino-Mayer and Swetnam 2000, Donnegan et al. 2001, Schoennagel et al. 2004). In the northern Rocky Mountains, Koehler (1990a, b) suggested that hare abundance has declined as a result of fire suppression and a subsequent shortage of young lodgepole pine forests. This premise is supported by the large proportion of forests that are dominated by mature lodgepole pine forests in western North America (Koch 1996), which includes an age-class distribution of lodgepole pine stands in the central Rocky Mountains that is skewed toward mature and overmature stands (Long 1995). In the Colorado Front Range, a dramatic decline in fire frequency was documented in the montane zone (*ca.* 1830 – 2790 m) beginning in the early 1990's (Veblen 2000, Veblen et al. 2000, Donnegan et al. 2001). At mid-elevations, there has been a dramatic decline in fire in the Medicine Bow Range in south-central Wyoming since the early 1900's (Kipfmüller and Baker 2000), and in lodgepole pine forests of the Sawatch Range in central Colorado (Zimmerman and Laven 1984). Fire suppression in forests that tend to be in the low or mixed-severity zone appears to have given rise to an increase in the density of relatively fire-intolerant and shade-tolerant species such as Douglas-fir, and a decline in early successional lodgepole pine forests (Schoennagel et al. 2004).

Conversely, human influences on fire regimes have apparently played less of a role in high elevation forests than in lower elevation forests in the southern and central Rocky Mountains, and it is less likely that fire suppression has affected hare abundance in these forests. The effectiveness of fire suppression over the past century is believed to be low in forests characterized by a high-severity fire regime, including spruce-fir and higher elevation lodgepole pine forests (Sherriff et al. 2001, Schoennagel et al. 2004). Instead, fire occurrence at high elevation sites is mainly associated with drought conditions (Sherriff et al. 2001). Schoennagel et al. (2004) argue that current fire patterns in subalpine forests are marked by infrequent, high-severity and stand-replacing fires that “are ‘business as usual’ in this forest type, not an artifact of fire suppression.” The extensive 1988 Yellowstone fires, for example, apparently had little to do with suppression because fires were actively suppressed on a large scale only from 1950 to 1972 (Turner et al. 1994, Schoennagel et al. 2004), and the time period

prior to this without a stand-replacing fire was not unusual (Anderson et al. 2004).

Wildland development

Conversion of subalpine forest due to housing development, road building, and ski-area expansion reduces the overall area of snowshoe hare habitat. Unlike forests that are managed for timber productivity, clearing these areas permanently removes hare habitat. Because hares tend to avoid broad, open areas, wide, linear ski runs may decrease effective habitat patch size, reduce habitat connectivity, and increase exposure of hares to predation. Although most development has more of an impact on a local scale, the primary question is whether removal of hare habitat, particularly high quality habitat, impacts Canada lynx. Hare populations in the Rocky Mountains may be near the minimum threshold required by lynx (Steury and Murray 2004), and incremental loss of hare habitat could have long-term consequences for lynx. Thus, an investigation of region-wide cumulative effects of development-related habitat loss is warranted.

Snowmobile trails

Snowmobile trails are not likely to influence regional hare populations, but there is concern that trail compaction could allow certain predators (especially coyotes) to have access to deep snow environments that they would otherwise avoid (Ruediger et al. 2000). The fear is that coyotes would then compete with lynx for snowshoe hare, and Buskirk et al. (2000) suggested that the usual spatial segregation of lynx and coyotes during winter “may break down where human modifications to the environment increase access by coyotes to deep snow areas.” Two studies suggest that coyotes use trails more than expected (Bunnell et al. 2004, Kolbe 2005), but coyotes in Montana used snowmobile trails for less than 8 percent of their travel, and they used compacted and uncompacted forest roads similarly (Kolbe 2005).

Mining and fossil fuel exploration and development

No studies have examined population-level effects of mineral and fossil fuel extraction on snowshoe hares. However, at an industrial level, these processes alter and remove forested land cover, which could lead to reductions in local hare populations and reduced connectivity among hare populations in increasingly fragmented forests. In addition, road building and increased vehicle traffic could alter movement patterns and increase human-cause hare mortality. Finally, a

potential detriment to hares and their predators could occur through bioaccumulation of toxic substances (e.g., trace metals), as the result of mining activities. To date, however, results are inconclusive from the only study that has examined the relationship between mining activity and hare tissue concentrations of trace metals (zinc and cadmium; Zahratka 2004).

Sport harvest

At current levels, hunting pressure in Colorado and Wyoming is unlikely to affect snowshoe hare populations. Although bag limits are high (Colorado: 10 hares per day; Wyoming: 4 hares per day) and the hunting season is long (September – February), the most recent reports (2003) of annual harvest estimate that only 410 hares were harvested in Wyoming (Wyoming Game and Fish) and 1,532 hares in Colorado (Colorado Division of Wildlife).

Conservation Status

Trends in abundance and distribution

Until recently, very little attention has been paid to the population status of hares in the Rocky Mountains because they are widely distributed within mid- to high-elevation forests. As a result, no data exist indicating that hare population size has changed. Likewise, there is no evidence that the distribution of snowshoe hares has contracted, at least at a regional scale.

It is concerning, however, that Canada lynx populations in the Rocky Mountains have declined over the past century. Although lynx populations have been negatively impacted by a range of factors in the Rocky Mountains (Ruediger et al. 2000, Ruggiero et al. 2000), lynx are so closely tied to snowshoe hare density, that changes in lynx abundance could indicate that, at least in part, hare abundance and distribution has also declined.

One possibility is that the amount of prime hare habitat (i.e., mature spruce-fir and young lodgepole pine forests) has eroded over the past century. There is concern throughout the Rocky Mountain region that the abundance of young lodgepole pine forests has declined due to fire suppression (Koch 1996). Indeed, the area burned each year by wildfires was relatively low for much of the 20th century (Grissino-Mayer and Swetnam 2000, Schoennagel et al. 2004). It also is likely that the extent of spruce-fir forests within Region 2 has declined. Cumulative effects of timber extraction, road building, ski-area development, and urban development

have reduced the abundance of old-growth spruce-fir forests. Although substantial expanses of spruce-fir forest remain in many parts of Colorado and Wyoming, we suspect that many areas of prime hare habitat have been heavily impacted because development is often concentrated in areas with thick forest and more gentle slopes, and timber extraction heavily targets diverse old-growth stands. Whether or not these impacts have removed enough hare habitat to precipitate changes in lynx abundance is debatable, but the possibility remains that without careful management of spruce-fir forests, lynx recovery efforts could be compromised long-term.

Management Approaches for Snowshoe Hares in Region 2

Implication and potential conservation elements

Conservation of abundant and widespread snowshoe hare populations is a priority to maintain the ecological integrity of subalpine Rocky Mountain forests, and to achieve conservation and recovery of the Canada lynx. Hares are found in several habitat types, they impact woody plant communities, and many predator species rely on hares during the winter because they are one of the few small mammals to exist in the supra-nivean environment. Although snowshoe hares are common and not in imminent danger within Region 2, there is cause for concern for the future of a well-distributed and relatively abundant hare population. Landscape-wide forest conditions and prime hare habitat in the Southern Rocky Mountains are threatened by climate change, certain forest management practices, and loss and fragmentation of habitat to development. Moreover, there is a diversity of threats to hares that could cumulatively affect their population security.

A key to understanding hares in the Rocky Mountains is the realization that this population is probably more sensitive to environmental change and habitat fragmentation than hares in other areas because they are at their southernmost geographical extent. Rocky Mountain hares persist along a geographic peninsula of sorts, and they are confined to subalpine forests that are naturally fragmented and bounded by areas of non-habitat. Topography, disturbance history, geology, vegetation, and weather patterns are highly variable over short distances in these mountains, resulting in a mosaic of habitat conditions for snowshoe hares, variable patterns of hare distribution and abundance, and barriers to dispersal. A good example of this heterogeneity can be seen in the north end of Yellowstone National Park (**Figure 13**) where patches of



Figure 13. A regenerating lodgepole pine forest from the 1988 fire surrounded by grasslands and sagebrush, older lodgepole, and the steep slopes of Bunsen Peak in Yellowstone National Park near Mammoth Hot Springs, Wyoming.

young lodgepole pine suitable for hares are surrounded by open shrub, older forest, and steep slopes.

Landscape variability has substantial implications for hare ecology and population biology. For example, the juxtaposition of high and low quality habitat and the lack of interconnectedness among populations are probably major reasons why hare populations do not appear to rise and fall synchronously across large areas (Griffin 2004). We also suspect that the ecological importance of hares can vary over short distances concomitant with changes in elevation and forest type. From the standpoint of the Canada lynx, the spatial arrangement of prime hare habitat is probably a key element influencing lynx reproduction, social cohesiveness, and ultimately population viability. It is of chief concern that lynx viability is limited by the capacity of the landscape to sustain prime hare habitat. Indeed, further contraction or degradation of prime forests would create an increasingly isolated and patchily distributed hare population, particularly at low elevations in warmer and drier forests and in more rugged terrain where populations are already fragmented. Negative impacts of further fragmentation could include lower overall density, impaired dispersal, and concentrated hare populations that are more vulnerable to predators (for potential impacts of

fragmentation see Wolff 1980, 1981, Keith et al. 1993, Wirsing et al. 2002a, Griffin 2004).

Disturbance events such as wildfire and timber harvest are the main causes of habitat change and fragmentation in subalpine forests (Peet 2000, Veblen 2000). Generally, disturbance is considered to benefit hares because they have a strong association with regenerating forests. However, forest managers need to be aware that disturbance has a range of temporal and spatial effects on hares, and these depend on forest type and the environmental conditions that influence tree regeneration. Specifically, fire and logging can have decidedly different roles within lodgepole pine and spruce-fir forests, the two primary Rocky Mountain habitat types occupied by snowshoe hares. Disturbance of mature lodgepole pine forests, and subsequent regeneration of dense young lodgepole pine, has proven to be a beneficial process for hares in the northern and central Rocky Mountains (see Habitat use in the Rocky Mountains section), and we believe that disturbance (particularly wildfire) will benefit hares in the southern Rocky Mountains as well. However, we suspect that disturbance in spruce-fir forests over large areas (e.g., clearcuts or stand-replacing wildfire) can be detrimental because these forests are slow-growing and regeneration often takes several decades before

trees are tall and dense enough to provide hares with ample food and cover during the winter (Wolfe et al. 1982). Alternatively, small-scale or patchy disturbance patterns in spruce-fir forests might be beneficial because small openings promote growth of shrubs and small trees favored by hares, and habitat connectivity would not be compromised. There is very little information available about specific hare/habitat relationships and disturbance scenarios in either spruce-fir or lodgepole pine forests in the southern Rocky Mountains, however, and substantial research is needed to better guide management strategies.

A potential looming threat to hare populations in Region 2 is climate change. Although climate change is beyond the effective scope of forest and wildlife managers, it is important that the link between forest composition, forest health, disturbance intervals, and climate change be closely monitored over the next few decades. Forest management strategies should be designed with the base understanding that spruce-fir forests are likely to shrink (Romme and Turner 1991), but young lodgepole pine forests may actually increase if disturbance intervals are shorter. Increased disturbance through fire and silvicultural treatments in lodgepole pine forest will likely benefit hares in some areas. However, the corresponding loss of mature spruce-fir forest could have wide-ranging ecological effects on hares, at least in Colorado where these forests appear to be important to hares. We recommend, therefore, that preservation of mature spruce-fir habitat should be a high-priority, particularly at the southernmost extension of the hare's range.

Tools and practices

Landscape models of hare abundance

A primary conservation tool for managing animal populations is development of geospatial models that predict distribution and abundance patterns. An important example is GAP analysis, a coarse habitat association method that uses the distribution of vegetation classes and Geographic Information System (GIS) technology to predict the distribution of vertebrates and other taxa (Scott et al. 1993). In Wyoming and Colorado, GAP models have been produced for snowshoe hare (**Figure 3**). One benefit of such models is that landscape-level management questions can be addressed. For example, how widely dispersed are highly preferred habitats within Colorado and Wyoming and to what degree are they connected? The utility of these GAP models is primarily at a regional scale, however, and more specific information

concerning the relative quality of different habitats is necessary to produce finer-scaled estimates of hare distribution and density in the Rocky Mountains. To this end, we emphasize the need for studies at the scale of an individual forest that measure hare density in a range of potential habitats that considers dominant tree species, stand age, tree density, and other physio-environmental factors.

Monitoring hare abundance, density, and habitat use patterns

Mark-recapture, pellet surveys, and winter track counts are the most common methods used to estimate hare abundance. The appropriateness and labor intensity of these techniques vary, and careful consideration should be given to study goals concerning the level of understanding desired at different spatial and time scales. Mills et al. (2005) recommend a step-wise approach to estimating hare abundance across large spatial scales in the western continental United States. Areas of relatively low, medium, and high hare density should first be identified using fecal pellet counts, and subsequently, mark-recapture methods should be used in relatively high hare density areas to more explicitly examine absolute densities over time and space (Mills et al. 2005). Because hare populations are typically patchy in the western United States, this strategy enables researchers to focus on those areas with more abundant hares and to circumvent methodological problems associated with converting low pellet frequency to density.

The fecal pellet plot method is well suited for examining hare population abundance at large spatial scales because it is quick, simple, and relatively inexpensive. The density estimation method, first developed in the southwest Yukon (Krebs et al. 1987, 2001b), involves clearing hare fecal pellets from pre-existing plots rectangular plots (5.08 x 305 cm) and re-counting pellets on the same plots after one year. Clearing plots ensures that all pellets counted are from the past year; estimates derived from uncleared plots are unreliable because pellets may persist for several years (Prugh and Krebs 2004, Murray et al. 2005). Fecal pellet counts can be converted to density estimates via a Yukon regression equation (Krebs et al. 1987, 2001b), but there is concern that this equation may not hold for all areas of the hare's distribution. Hare defecation rates, and pellet loss and decomposition rates can vary with climate, habitat, and diet (Prugh and Krebs 2004, Murray et al. 2005), and large regional differences in diet and habitat use suggest that the relationship between pellet counts and hare abundance could vary geographically. Current

debate centers on whether Yukon rectangular plots or circular plots should be used to estimate low-density hare populations (McKelvey et al. 2002, Murray et al. 2002, Mills et al. 2005). Circular plots have a lower perimeter:area ratio than do long, skinny plots and, therefore, observers make fewer potentially biased decisions about whether to count pellets near the edge of the plot when using circular plots. In Idaho and Montana, circular (1 m²) and Yukon rectangular plots were comparable at estimating hare abundance (Murray et al. 2002, Mills et al. 2005). However, Murray et al. (2002) argued that circular plots showed an advantage over rectangular plots because they had a lower sample variance and required less time to establish in the field (Murray et al. 2002). Conversely, Mills et al. (2005) recommends that rectangular plots and the well-established Yukon regression should be used until a formal double-sampling study is performed.

An additional concern with the pellet plot method is that all fecal pellets deposited by hares do not necessarily persist for one year. Annual degradation rates range from 1 to 14 percent in Alaska (Prugh and Krebs 2004) to 20 to 75 percent in northern Idaho (Murray et al. 2005), and forest moisture conditions and the season of deposition (summer vs. winter) affect degradation rates (Prugh and Krebs 2004, Murray et al. 2005). Habitat biases in degradation rates could be corrected for if pellet decay in different habitats and moisture gradients is examined along with pellet count surveys (Murray et al. 2005). Seasonal pellet decay patterns should be accounted for by synchronized collection efforts to the fullest extent possible, and we recommend that counts include a distinction in the number of summer and winter pellets.

Mark-recapture techniques are highly recommended as a direct and well-developed method of estimating hare density over a relatively small area (Mills et al. 2005). Hares are live-trapped, marked and released, and population estimates are based on proportions of captures and recaptures during trapping periods. Typically used are standard mark-recapture estimators such as Jolly-Seber and other estimators available from PROGRAM CAPTURE (Rexstad and Burnham 1991). Estimations also can be derived based on minimum number alive (MNA; Murray et al. 2002, Wirsing et al. 2002a), which are best used when hare densities are low (Krebs et al. 1986). Mark-recapture estimates are improved when they are combined with information from radio-monitored hares so that untrappable animals can be removed from the estimate (i.e., dead or dispersed hares; Murray et al. 2002). Also, individual response to trapping and the effects

of environmental variables on trapping success, such as weather or moon illumination (Gilbert and Boutin 1991, Griffin 2004, Zahratka 2004) should be further evaluated to improve the conversion of population size estimates to hare density.

Winter track counts are useful as indices of hare abundance and to determine habitat use patterns (Hartman 1960, Litvaitis et al. 1985b, Bartmann and Byrne 2001, Zimmer 2004), and counts correlate well with other techniques (Litvaitis et al. 1985b, Thompson et al. 1989). However, winter tracks are not appropriate for measures of density. An obvious disadvantage of winter track counts is that they can only be conducted during periods of snowcover, and snow conditions affect track observability. Murray (2003) also mentions that tracks from other leporids might confuse counts, and travel patterns and track density may be inconsistent across the landscape if social interactions, predator densities, or food abundance affect movement.

Habitat management

Fire and timber harvest are the two most important habitat management tools because they can be used at a landscape scale to improve hare habitat by converting mature forests to early successional stages. However, effects of fire and timber harvest on hare abundance range from detrimental to beneficial, and careful consideration should be given to forest type, treatment intensity, and the time frame and spatial scale over which responses are measured. As a rule of thumb, the critical factors that ultimately determine whether logging or fire are beneficial are species composition, tree density, and rate of tree growth in regenerating stands.

Silviculture: Snowshoe hares are abundant in many early to mid-successional forests, and timber harvest is a mechanism for cycling young stands into the landscape. However, the specific timber management practices (i.e., clearcut, selective harvest, or pre-commercial thinning), locations, tree species constituents, harvest size, and ecosystem dynamics associated with logging are highly variable, and potential impacts on hares can range from highly beneficial to detrimental. It also must be recognized that the suitability of post-harvest stands changes temporally, and thus the overall treatment effects cannot be sufficiently evaluated over a short time frame.

In clearcuts, habitat conditions are poor for several years post-harvest, and hare density may not rebound for 10 to 30 years depending on forest regeneration (Parker

1984, Litvaitis et al. 1985a, Monthey 1986, Newbury and Simon 2005). Because of the poor environment for hares immediately following harvest, the larger landscape should retain forested stands in more optimal condition to maintain hare populations and to be a source for future recolonization. To achieve this goal in timbered lands, close attention should be paid to harvest rotation, tree density, and forest regeneration capacity. However, the landscape matrix of mature and regenerating forest that is necessary to maximize hare populations is mostly speculative (Ferron et al. 1998, de Bellefeuille et al. 2001). Compounding this uncertainty, Rocky Mountain forests are heterogeneous, variable in regeneration capability, and have different spatial patterns of forested versus non-forested habitat, such that it is impossible to prescribe a single management scheme. Unfortunately, specific interactive effects of forest type, environmental variables, and harvest technique on snowshoe hares have not been well studied in the Rocky Mountains. Conversely, we do have a good grasp of what constitutes high-quality hare habitat. We know that dense woody understory cover is very important to hares, and that certain species are more valuable to hares as winter foods than others. There also exists a large body of knowledge about regeneration post-harvest in a range of forest types and silvicultural methods, and we use this information to make inferences about potential benefits of harvest, to identify negative consequences, and to make management recommendations.

Buffer strips and pre-commercial thinning:

A management technique that may alleviate the initial negative effects of clearcutting is to provide adjacent forested stands or buffers in quality habitat condition. Partial-cuts have proven to benefit some other small mammals in subalpine forests (Klenner and Sullivan 2003), and dense, small clumps of forest may provide suitable hiding cover, enable some hares to survive until forests regenerate, and provide a source for recolonization of clearcuts (de Bellefeuille et al. 2001). Hares used riparian forest strips that were adjacent to clearcut stands in Quebec (Darveau et al. 1998), and hares frequently use forests with much habitat interspersion, especially around clearcut edges with dense understories (Conroy et al. 1979). In Washington, residual patch size was positively correlated to pellet counts (Thomas et al. 1997), and it was recommended that buffer strips should be over 100 m to maintain hare density (Potvin et al. 2005b).

Attention has also recently been paid to mitigating the potentially adverse effects on hares of pre-commercial thinning (see Threats section).

One proposed mitigation measure is to leave thinned trees and branches on the ground as cover and food (Sullivan and Moses 1986, Bull et al. 2005). However, this technique has not always enhanced hare survival in thinned areas (Cox et al. 1997), and it likely has only short-term benefits in any case (Sullivan and Sullivan 1988). A more promising conservation tool is to reserve unthinned patches within thinned areas, but the appropriate size and configuration of reserves have only been evaluated in three studies (Griffin 2004, Ausband and Baty 2005, Bull et al. 2005). In Oregon, hare abundance was examined in relation to a thinning regime in 25 to 40 year old lodgepole pine stands that ranged in size from 12 to 33 ha (Bull et al. 2005). Hare abundance tended to be highest in unthinned stands and in patch cuts (10-meter cleared circular patches surrounded by unthinned areas 10 to 50 m wide), and lower in corridor cuts (alternating thinned and unthinned stands that were 20 to 200 m wide). Patch cuts appear to be a suitable thinning technique for maintaining hare populations, but the inconsistent width of thinned corridors confounds interpretation of this approach (Bull et al. 2005). In mixed conifer forests in Montana, hares used thinned stands with reserves (where 20 percent of the total area was retained in uncut 0.25 ha patches) more than thinned stands without reserves (Griffin 2004). However, these reserve stands did not prevent a decline in hare density relative to controls, and it was suggested that reserves should be larger to maintain hare abundance (Griffin 2004). Also in Montana, hare populations increased more after treatment in unthinned stands than in thinned stands, but the size of retention areas (8 percent and 35 percent) did not affect hare relative abundance (Ausband and Baty 2005). These data indicate that unthinned reserves are important to hares, but Ausband and Baty (2005) argue that the small size of the thinning areas (10.15 to 14 ha) may have reduced the beneficial impacts of reserves because hares could access adjacent forest.

Lodgepole pine forests: Lodgepole pine forests in Colorado and Wyoming are managed for timber production, recreational interests, and wildlife. The two major processes involved are timber harvest of older trees and stand density management. Both of these practices have high potential to impact snowshoe hares because the relationship between hares and lodgepole pine is dependent on interactions between stand structure, age, and site type (Sullivan and Sullivan 1988, Koehler 1990a, Thomas et al. 1997, McKelvey et al. 2000b).

Clearcutting older lodgepole pine forests can be highly beneficial to hares if the site regenerates at

sufficient density, but we caution managers that the relationship of young lodgepole stands to hares in the southern Rocky Mountains has not been studied. In the northern Rocky Mountains, the relationship between hares and young lodgepole pine is well established, and Koehler and Brittell (1990) recommend that clearcuts should be a minimum of 20 to 25 acres but not more than 40 acres (also see Thomas et al. 1997). Their reasoning is that for hares to fully use clearcuts as they regenerate, the cuts must be at least equal to the size of a minimum hare home range, but they should not be too large because recently cut areas are essentially non-habitat, potential barriers to movement, and hares do not utilize habitat in the interior of clearcuts (Brocke 1975, Conroy et al. 1979, Potvin et al. 2005b). However, individual clearcuts of this size would have little effect on forest-wide hare populations. To improve habitat conditions at the landscape level, it is necessary to maintain a network of stands in a younger age class. We recommend these stands be separated by no more than 2 km, which is within the dispersal range of hares in the western United States (see Movement patterns section).

Key factors in successful regeneration of harvested lodgepole pine forests include the usual interactions among environmental variables such as slope, aspect, elevation, soil conditions, and climate, as well as the degree of serotiny (late-opening cones) expressed in a stand. Serotinous cones can range from a few million per acre to virtually none (Muir and Lotan 1984). Generally, more recently burned, younger stands have more serotinous cones. It is easier for forest managers to control restocking in stands with abundant serotinous cones because seeds can be dispersed during slash removal and many cones on or near the ground are opened by normal summer soil surface temperatures (Lotan 1964). Alternatively, seedfall from non-serotinous cones is more difficult to manipulate, and must be wind-disseminated. Under these conditions, the size and shape of cutting units and heights of trees in adjacent stands become important considerations (Long 1995).

In regards to pre-commercial thinning in lodgepole pine, the early stages of stand development density are clearly important for hares, but in older stands hares are more abundant in open lodgepole forests that have a significant understory component than in dense, self-pruned stands with little productivity. Major management considerations, therefore, appear to be somewhat contradictory. Should managers cultivate well-stocked young stands that hold dense but transient populations of hares, or thin stands and

promote development of well-spaced stands that have lower but more long-lasting hare populations? Given that rigorous long-term experimental studies are lacking, we recommend two potential strategies: 1) thinned forests should meet criteria for minimum stem density requirements (>5000 stem per ha; see Habitat use section), and/or 2) unthinned reserves should be left within thinned areas. Because recommended tree density post-thinning is significantly greater than tree spacing typically applied in pine forests in the western U.S. (Barrett 1995), and it is doubtful that thinning to this level, per the first strategy, would have commercial benefit (Long 1995), it is likely that most forest managers will opt for the second strategy. However, we refer back to our earlier discussion, and caution managers that the best size and configuration of unthinned reserves is not yet certain.

Engelmann spruce/subalpine fir forests:

High-elevation forests are projected to be a major source of timber over the next several decades, and the sustainability of clear-cutting in subalpine forests is under scrutiny (Vyse 1999). For hares, there are reasons to believe that the impacts of clearcutting in spruce-fir forests are mostly negative, and that initial and future habitat suitability declines as clearcut size increases (see Threats section). For hares, the suitability of clearcuts as future hare habitat depends on the effectiveness of tree regeneration, which is influenced by the size of clearcuts and the site environment (Alexander 1987, Coates 2002). We recommend small patch cuts (e.g., ~ 1 ha; see Parish and Antos 2005) to promote regeneration, partly because spruce and fir establishment declines with distance from a seed source at the boundary of the cut (Noble and Alexander 1977, Noble and Ronco 1978, Feller 1998, Lajzerowicz et al. 2004). We believe small cuttings in spruce-fir forests will benefit hares because these more closely mimic the size of natural gap disturbances that promote growth of shrubs and small trees (Oliver and Larson 1986). Cuts in unprotected sites, steep slopes, erodible soils, or south-facing aspects should be avoided because it is sometimes difficult to establish seedlings in these areas (Noble and Alexander 1977, Feller 1998, Lajzerowicz et al. 2004). Management techniques such as group selection or shelterwood have proven helpful (Long 1995), although these do not necessarily ensure successful regeneration following timber harvest (Lajzerowicz et al. 2004).

Fire management: Stand-replacing wildfire can improve snowshoe hare habitat once regenerating forests are reestablished, because a dense growth of early successional species are often favored by hares for food and cover. The benefits of fire are particularly

noticeable in lodgepole pine forests, where regenerating young stands are generally far more valuable to hares than mature forests. We highly recommend that a focus of forest management should be restoration of natural fire patterns. Despite this recommendation, fire in subalpine Rocky Mountain forests does not always result in suitable conditions for hares. Lodgepole pine regeneration processes are highly variable and not always beneficial, and fire within the spruce-fir zone can be detrimental to hares. Therefore, appropriate fire management strategies in the subalpine zone should be adaptive and built on an understanding of specific regeneration scenarios.

After stand-replacing fires, lodgepole pine can regenerate in dense, even-aged stands that are favored by snowshoe hares. Patterns of lodgepole regeneration vary widely, however, and fire is less valuable to hares when lodgepole pine is not reestablished in sufficient densities. Although the fires of 1988 in Yellowstone National Park successfully converted mature to young lodgepole pine forest, regeneration was not homogenous and favorable conditions for hares fluctuated substantially (E. Ellsworth personal observation; K.E. Hodges personal communication 2005). Post-fire lodgepole forests in Yellowstone ranged from 0 to 500,000 lodgepole stems/ha, and most stands were below 5000 stems/ha (Kashian et al. 2004, Turner et al. 2004), which is roughly the minimum required by hares (see Habitat use section). The best explanation for this variability is that seed supply differed throughout the forest as a result of two main factors: fire intensity and the level of cone serotiny. Fire intensity is important because crown fires destroy many cones and the result is high seed mortality and often poor or delayed seedling regeneration (Anderson and Romme 1991, Turner et al. 1997, 1999, Anderson et al. 2004). Serotiny is important because these late opening cones release their seed when heated by lower intensity fires, and they can release enormous number of seeds across freshly prepared seedbeds. Alternatively, if most cones are non-serotinous, which tends to be the case in older stands at higher elevations (Schoennagel et al. 2003, Anderson et al. 2004), a similar flush of an abundant seed source does not occur, and post-fire seedling density is much lower. Consequently, it is likely that the benefits of fire to snowshoe hares are highly dependent on pre-fire lodgepole pine forest conditions. Before developing management schemes, careful consideration should be given to important determinates of stand regeneration that we discussed above, namely degree of serotiny, risk of high-intensity fires, as well as environmental variables such as elevation, aspect, and slope.

Information Needs

What is the minimum hare population necessary to support Canada lynx?

Steury and Murray (2004) modeled lynx persistence in northern forests based on hare density, but the relationship between hare density and lynx demography has not been robustly examined in the southern Rocky Mountains. This is a concern because lynx in the southern Rocky Mountains may require fewer hares due to dietary potential, and energetic and behavioral differences. A field-based understanding of minimum hare requirements for lynx in the southern Rocky Mountains would represent a substantial step forward because it would allow for better identification of suitable habitat and limits to lynx population size. To this end, we strongly encourage that transplanted lynx be used to study diet dependency on hares, energy requirements, hunting behavior, and spatial relationships. Free-living lynx are difficult animals to capture and study, and the large number of radio-collared animals in Colorado provides a unique opportunity to investigate a specialist predator and its prey at the periphery of its range. As a cautionary note, however, it must be taken into account that transplanted boreal lynx did not evolve in the southern Rocky Mountains, and it may take several generations for this population to adapt behaviors and hunting patterns that are more suitable to this habitat and representative of native lynx.

What factors limit hare populations in the southern Rocky Mountains?

Southern hare populations appear to be limited by an interaction between patchy habitat and an abundant and diverse guild of generalist predators (Dolbeer and Clark 1975, Wolff 1980, 1981, Buehler and Keith 1982, Keith et al. 1993, Wirsing et al. 2002a). Metapopulation and source/sink models have been invoked to explain southern hare population dynamics (Keith et al. 1993, Wirsing et al. 2002a, Griffin 2004). However, there are some key elements that remain to be explored before a better picture is formed of limits on hare abundance. A significant missing factor is a measure of the relative degree of connectivity that exists among subpopulations. It is unknown to what degree the landscape is permeable to hare movements, and the genetic structure should be evaluated (Burton et al. 2002). It also is important to investigate the role of predators in this environment. How important are hares in the diet of generalist predators, and are hares really

subject to higher and more consistent predation rates? What sort of influence do topography and snow depth have on predation rates?

There also exist some questions concerning food resources. Food habits of hares have not been well explored in the southern or central Rocky Mountains, and no research has been conducted here on the abundance or nutrition of hare food. Although the relatively low densities of hares in these mountains suggest that the gross quantity of woody browse is unlikely to be a limiting factor, even during the winter, it is possible that hare populations might be larger in areas with higher-quality food resources. To test food/hare relationships, regional and age-specific variability in nutrients and forage chemical defenses should be examined, particularly as a function of hare density and browsing rates. Furthermore, the influence of summer nutrition on body condition and reproductive rates should be examined.

Habitat associations

Spruce-fir forests are important hare habitat in the southern Rocky Mountains, but patterns of hare abundance are not well studied. To fill knowledge gaps in critical ecological processes and to develop a defensible forest management scheme, we recommend that researchers address the interactive effects of stand structure, age, site type, and disturbance on hare populations. Variables such as elevation, slope, or aspect might prove to be important because they influence snow depth, species constituents, and tree spacing, which in turn might affect dynamics with predators and influence food availability. Likewise, we know very little about how hare abundance changes over time in these forests, and we suggest that both manipulative and natural studies be used to compare different regeneration scenarios. Although fire and timber harvest appear to be largely detrimental because hares are associated with mature spruce-fir forests, it remains important to identify possible mitigating scenarios.

Young, dense, lodgepole pine forests represent high-quality habitat for snowshoe hares in the central and northern Rocky Mountains, but thus far, the nature of the relationship between hares and lodgepole pine

forests in Colorado are limited to studies in mature stands (Zahararka 2004) or stands that lacked sufficient density (Miller 2005), both of which are characteristically less valuable to hares. We suggest that a top research priority is to focus on hare abundance patterns by plant community, age-class, and stem density in southern Rocky Mountain lodgepole pine forests. Does the importance of lodgepole pine to hares differ by plant community, or does it depend on whether it is a minor seral species versus a dominant seral or climax species? This could be an important line of research in Wyoming and Colorado, where the ecology of lodgepole pine is highly variable. For example, the successional role of lodgepole pine changes with elevation in the Colorado Front Range, from mainly a seral species at lower and upper altitudes or its range, to a dominant climax or prolonged seral stage at intermediate elevations (Moir 1969). Studies also should incorporate the impact of wildfire and timber harvest on hare abundance in lodgepole pine forests. Pre- or post-fire studies have not been conducted in the Rocky Mountains, comparative analyses among habitat types after a fire have not been done, and our current understanding of the population response of hares to fire is limited to inference from studies conducted in regenerating forests in the northern and central Rocky Mountains. Considering timber harvest, two key issues are 1) the landscape matrix that best ensures abundant hare populations, and 2) development of a better index of long- versus short-term impacts of logging. Is it more important to promote the growth of dense stands of lodgepole pine that are initially higher quality, but possibly more ephemeral, or more spaced forests that might house lower density but longer-lasting populations? It should be kept in mind that the answer to this question might be related to the overall composition of the forested landscape at a scale greater than the harvest unit. Of what should the matrix of cut-over forests, regenerating stands, and mature forests be comprised to maximize hare abundance? After cutting, do enough areas of prime hare habitat remain to serve as a source for repopulating harvested stands? Finally, what harvest scenarios significantly reduce the permeability of the landscape to hares movement? To address these questions, we strongly recommend that impacts of harvest should be further evaluated experimentally in the field, and results used as a backbone of landscape modeling efforts.

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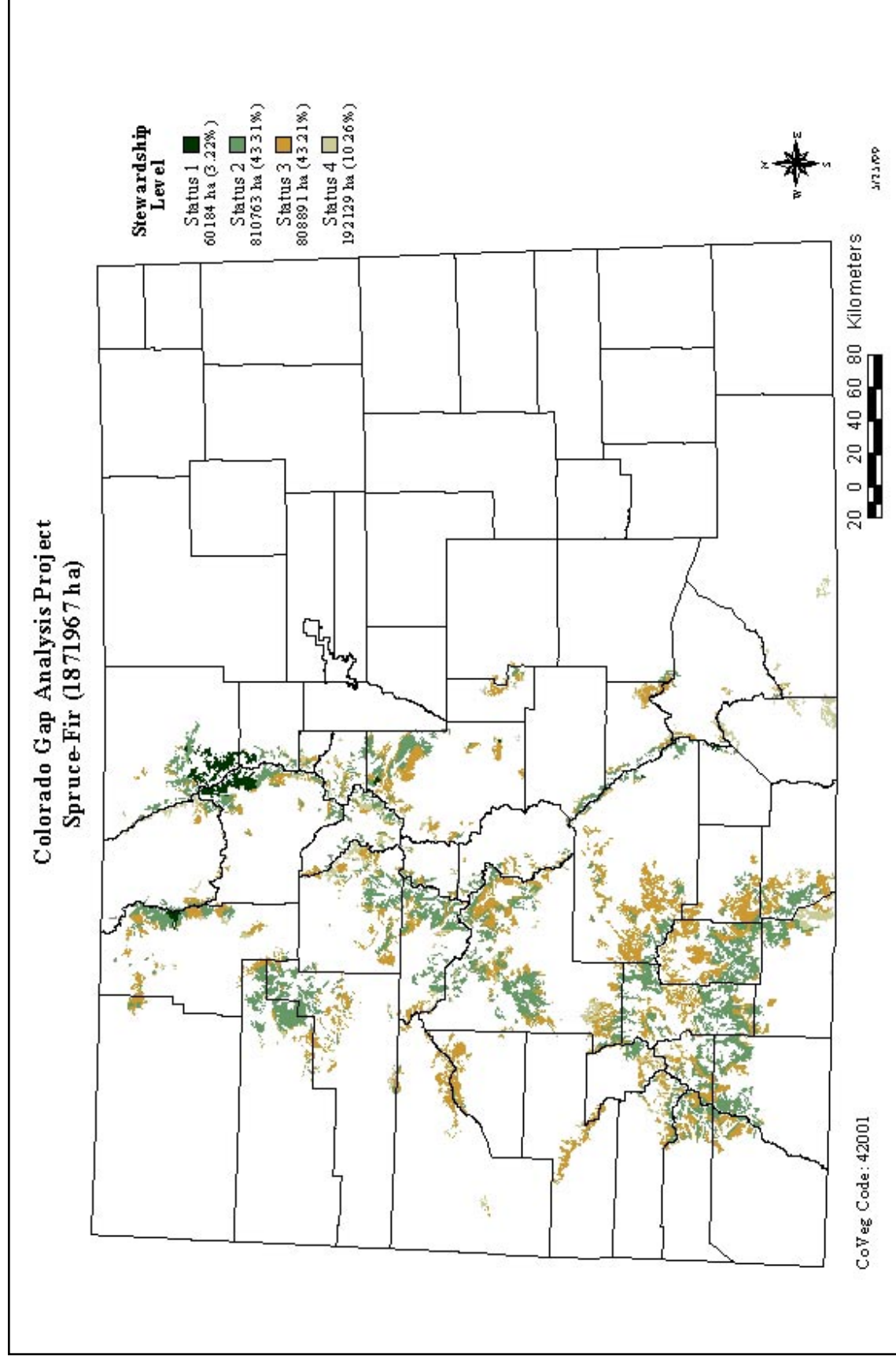
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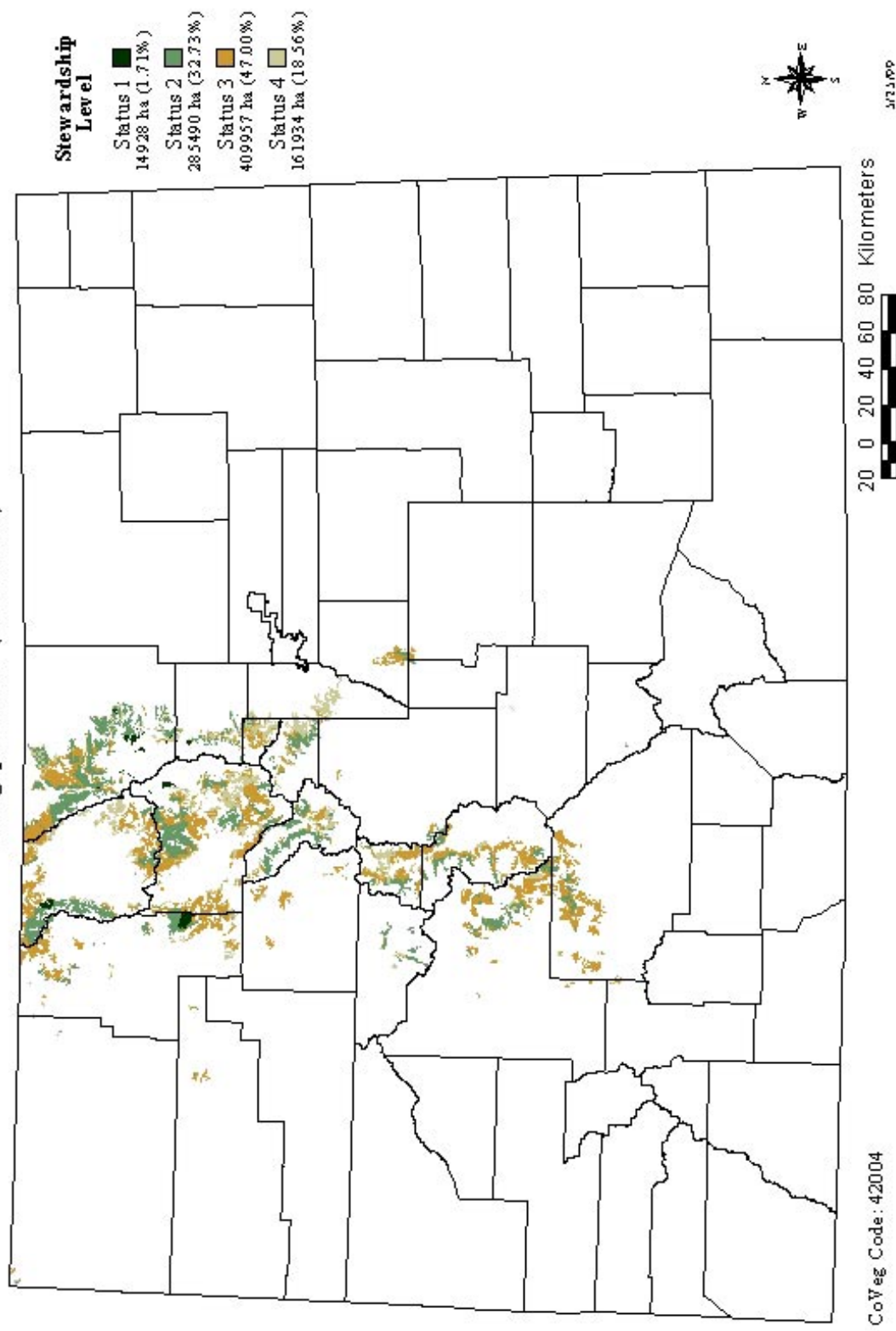
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APPENDIX

Distribution of spruce-fir and lodgepole pine forests in Colorado from Gap analysis (<http://ndis1.nrel.colostate.edu/cogap/veggapfrm.html>). These maps use a status of 1 through 4 to denote the relative degree of management for biodiversity maintenance for a particular tract of land, where “1” represents the highest, most permanent and comprehensive level of maintenance, and “4” represents the lowest, or unknown status.



Colorado Gap Analysis Project Lodgepole Pine (872309 ha)



LIST OF ERRATA

08/29/06 On March 21, 2006 the White River National Forest ammended their Forest Plan to revise their list of MIS. The snowshoe hare was not included on that revised list.

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